UNIVERSITÉ DU QUÉBEC À MONTRÉAL

# ÉVALUATION DES STRATÉGIES DE RÉTENTION DE BOIS MORT DANS LES BRÛLIS RÉCENTS SUR LE MAINTIEN DE LA DIVERSITÉ BIOLOGIQUE

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CHANTAL CLOUTIER

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# RÉSUMÉ

Les feux de forêt représentent la plus importante perturbation naturelle survenant en forêt boréale. Les brûlis qui en résultent contiennent du bois mort sur pied qui constitue un attribut d'habitat important pour la biodiversité. Ces brûlis sont toutefois convoités pour la récolte de bois afin de minimiser les pertes économiques reliées aux feux. La rétention de parcelles brûlées a donc été proposée pour mitiger les effets négatifs de cette pratique sur la biodiversité. Leur efficacité à maintenir cette dernière est toutefois peu documentée. L'avifaune utilisant les brûlis est très sensible à la coupe de récupération et peut donc servir d'indicateur pour tester l'efficacité de cette stratégie. Nous avons donc réalisé une étude visant à caractériser les communautés aviaires dans différents types de rétention contenant un large spectre de conditions pré- et post-feu dans le but de déterminer les impacts de la coupe de récupération sur cette communauté.

Ce mémoire comprend un chapitre rédigé sous forme d'article qui contient trois sous-objectifs. Le premier est de présenter l'ensemble de la variation de la communauté aviaire en fonction de différentes stratégies de rétention de bois mort (tiges isolées, bandes riveraines et parcelles de taille variable). Puis, l'étude cherche à identifier de façon plus spécifique les facteurs écologiques à de multiples échelles spatiales qui affectent la distribution de neuf espèces associées au bois mort (8 cavicoles – 1 corticole) dans les habitats brûlés résiduels. Enfin, l'étude a pour troisième objectif d'analyser la présence de cavités excavées par les trois espèces de pics (pic à dos noir, pic à dos rayé et pic flamboyant) les plus susceptibles d'utiliser la forêt brûlée résiduelle afin de vérifier comment les divers types de rétention affectent la persistance des populations de ces espèces dans le brûlis aménagé. Nos résultats indiquent que les divers types de rétention de bois brûlés n'ont pas tous la même capacité à maintenir la faune aviaire associée aux habitats post-feu. En effet, une analyse de communautés d'oiseaux a révélé que les rétentions en tiges isolées et en lisières boisées riveraines ne maintiennent pas aussi efficacement les espèces associées aux feux et sont plutôt composées d'espèces de début de succession, de jeunes forêts ou généralistes. À l'inverse, les parcelles faisant plus de 20 ha permettent de répondre aux exigences écologiques de plusieurs espèces associées aux feux telles que les espèces cavicoles primaires et secondaires. Les résultats des analyses indiquent également qu'il est important de conserver une diversité de conditions écologiques telles que la composition et la structure des peuplements avant feu et la sévérité du feu. Par contre, le maintien des espèces les plus sensibles à la

coupe de récupération repose sur la présence de sites de grande superficie contenant une forte densité d'arbres morts. Finalement, l'analyse des sites de nidification de trois espèces cavicoles primaires a montré que le pic à dos noir, le principal excavateur de cavités dans notre aire d'étude, sélectionne préférablement les rétentions de grandes superficies de forêts brûlées matures pour excaver ses cavités. Ainsi, un paysage possédant au moins 20 ha de forêts brûlées matures dans un rayon de 500 m permet à cette espèce de nicher et d'assurer le maintien de nombreuses espèces réutilisant subséquemment les cavités excavées. Le maintien d'essences décidues comme le bouleau à papier au sein des peuplements de conifères permet également au pic flamboyant de nicher dans le brûlis et ce, peu importe la taille de la parcelle de rétention.

**Mots clés:** feu, coupe de récupération, espèce cavicole, espèce corticole, rétention de bois mort, communautés d'oiseaux.

# INTRODUCTION

## *Le régime des feux en forêt boréale et ses impacts sur la diversité biologique*

En forêt boréale, les feux constituent la plus importante perturbation naturelle (Bergeron et al. 2001, Koivula et Schmiegelow 2007) et sont les principaux responsables de la dynamique forestière (Saab et Powell 2005). En effet, 5787 des 1.36 millions de kilomètres carrés de forêts boréales canadiennes aménagées brûlent en moyenne chaque année (Gauthier et al. 2014). Bien que la majorité des feux s'étendent sur moins de 1000 hectares, ce sont les feux de plus grande superficie (> 1000 ha) qui sont les principaux responsables de la succession secondaire. En outre, ces feux consument 90% de la surface totale brûlée annuellement (Bergeron et al. 2002). De plus, la fréquence des feux, quoique variable selon les régions, est considérée comme étant relativement courte. L'intervalle de retour est d'environ 70 à 150 ans dans les plaines et le bouclier boréal et augmente jusqu'à 500 ans sur la Rive-Nord de Québec et le Labrador (Foster 1983, Bergeron et al. 2004). Leurs configurations et intensités varient également en raison des conditions météorologiques (pluie, température, vent et saison) et physiques (topographique, type de sol et eau) du territoire (Rowe et Scotter 1973, Bergeron 1991, Kafka et al. 2001). La combinaison de ces facteurs génère une mosaïque de couverts forestiers où différentes proportions de forêts brûlées à divers niveaux se retrouvent à l'intérieur d'un même territoire brûlé (Kafka et al. 2001, Bergeron et al. 2002, Schmiegelow et al. 2006). Ainsi, par sa variabilité en intensité, en fréquence et en superficie, le régime des feux façonne le paysage forestier en influençant la structure d'âge et la composition des peuplements ainsi que la configuration des mosaïques forestières (Bergeron 2000, Bergeron et al. 2001, Bergeron et al. 2004).

En plus de façonner le paysage forestier, les feux génèrent des conditions uniques et fortement différentes des forêts non-brûlées (Smith 2000, Saab et Powell 2005). Ces forêts contiennent notamment du bois mort sur pied qui constitue un attribut d'habitat important pour plusieurs espèces animales (Smucker et al. 2005, Schmiegelow et al. 2006, Koivula et Schmiegelow 2007) et végétales (Purdon et al. 2004). Certaines espèces d'invertébrés, de vertébrés et de plantes sont d'ailleurs plus abondantes ou même uniquement présentes dans ces habitats (Nguyen-Xuan et al. 2000, Saint-Germain et al. 2004a, Hannon et Drapeau 2005, Schieck et Song 2006). Ce sont souvent des espèces associées ou dépendantes au bois mort. Parmi les invertébrés, nous retrouvons notamment les insectes saproxyliques (c'est-à-dire les insectes qui dépendent du bois mort pour compléter au moins une étape de leur cycle de vie; Saint-Germain et al. 2004b) qui sont dispersés dans les forêts âgées non brûlées, et rares ou inexistants dans les jeunes forêts, parterres de coupe et brûlis récupérés (Nappi et al. 2003, Nappi et al. 2010). Plusieurs espèces d'oiseaux se nourrissant de ces insectes ainsi que celles qui nichent dans les cavités sont également favorisées par la soudaine disponibilité de bois morts (Morissette et al. 2002, Hannon et Drapeau 2005, Saab et Powell 2005, Schieck et Song 2006). Parmi ces espèces, les pics du genre *Picoides* forment le groupe d'oiseaux le plus fortement favorisé par la disponibilité de bois mort sur pied qui leur sert à la fois de substrats d'alimentation et de nidification. En outre, les densités de pics dans ces habitats peuvent être de 40 à 80 fois plus grandes à celles observées dans les forêts non perturbées (Fayt et al. 2005). Les cavités excavées par ces pics sont ensuite réutilisées par plusieurs autres espèces d'oiseaux et de mammifères qui ne peuvent creuser une cavité mais qui deviennent des utilisateurs secondaires des cavités de pics (Martin et al. 2004). Ainsi, la forêt brûlée est à la base d'un réseau trophique dynamique qui inclut notamment les insectes saproxyliques et les pics. Ce réseau influence à son tour directement un second réseau fonctionnel d'espèces connu sous le nom de réseau d'utilisateurs de cavités. Ce réseau, qui inclut plusieurs espèces d'oiseaux et de mammifères, permet à

ces dernières de se maintenir à long terme dans la forêt brûlée en régénération (Drapeau et al. 2010).

En altérant la structure de la forêt, les feux entraînent une réorganisation des communautés fauniques (Smith 2000) qui favorisent plusieurs espèces au détriment d'autres (Drapeau et al. 2010). Outre les espèces cavicoles, les brûlis offrent également des conditions favorables aux insectivores aériens, au sol et sur l'écorce. En effet, les insectivores peuvent représenter plus de 75% des espèces présentes à un site brûlé (Morissette et al. 2002). Il en est de même pour les espèces nichant dans des nids fermés ou nichant au sol ou dans la canopée (Saab et Powell 2005). Les brûlis ne sont toutefois pas tous équivalents en termes de qualité d'habitat pour la faune puisque les feux génèrent une grande variabilité de conditions (Nappi 2009). En outre, plusieurs facteurs tels que la sévérité du feu, la maturité des peuplements, les essences d'arbres présentes et le temps écoulé depuis le feu sont susceptibles d'affecter la réponse des espèces au feu (Smucker et al. 2005, Kotliar et al. 2007, Nappi 2009).

*Écologie de l'avifaune en forêt brûlée*

En forêt résineuse brûlée de la forêt boréale, l'espèce de pic la plus abondante est le pic à dos noir (*Picoides arcticus*) (Nappi 2000, Hoyt et Hannon 2002, Koivula et Schmiegelow 2007). Les densités de pic à dos noir dans les forêts récemment brûlées sont d'ailleurs bien plus élevées que dans les forêts non brûlées (Hutto 1995, Nappi 2000, Hoyt et Hannon 2002). Cette espèce semble même être un spécialiste des forêts récemment brûlées (Hutto 1995, Murphy et Lehnhausen 1998, Nappi 2009) puisque sa productivité augmente dans ces habitats (Nappi et Drapeau 2009). De plus, les cavités qu'elle excave contrôlent la disponibilité des sites de nidification et abris pour les espèces cavicoles secondaires, ce qui en fait une espèce « clé de voûte » dans le système (Drapeau et al. 2009). Une seconde espèce de pic à répondre positivement au feu est le pic à dos rayé (*Picoides tridactylus*). Les deux espèces de pic colonisent

rapidement les forêts brûlées pour se nourrir d'insectes saproxyliques (Hannon et Drapeau 2005). Elles ont toutefois des exigences écologiques et des associations à des attributs d'habitat différentes ce qui fait que les deux espèces répondent à différentes conditions générées par le feu.

L'occupation des forêts brûlées par les pics dépend tout d'abord de l'abondance des insectes saproxyliques. Pour cette raison, il importe de comprendre comment la variabilité des conditions générées par le feu peut influencer ces invertébrés. Un des facteurs affectant le plus l'abondance de ces insectes est la sévérité du feu puisqu'elle affecte la quantité et la qualité du bois mort sur pied (Nappi et al. 2010). La présence d'insectes saproxyliques (notamment les familles des Cerambycidae, Buprestidae et Scolytinae) est généralement limitée aux premières années suivant la mort des arbres (Saint-Germain et al. 2004b, Boulanger et Sirois 2007). Plusieurs espèces dépendantes du bois mort répondent donc positivement à la soudaine disponibilité d'arbres morts qu'engendrent les feux de haute sévérité (Koivula et Schmiegelow 2007, Hutto 2008). En revanche, les feux de faibles intensités contiennent des arbres partiellement brûlés qui prennent plusieurs années à mourir (Gardiner 1957). La mortalité différée dans le temps de ces arbres a donc pour effet de maintenir les insectes saproxyliques dans les brûlis pour une plus longue période de temps après le feu (Nappi et al. 2010). Outre la sévérité du feu, la proximité à une forêt verte peut également augmenter l'abondance de certains insectes saproxyliques, tels que le longicorne noir (*Monochamus scutellatus*) puisque les adultes se nourrissent sur les aiguilles des arbres verts (Saint-Germain et al. 2004a).

À l'échelle de l'arbre, les arbres sévèrement carbonisés peuvent supporter une plus faible densité d'insectes saproxyliques que les arbres légèrement brûlés (Nappi et al. 2003, Saint-Germain et al. 2004b). Effectivement, les arbres légèrement carbonisés ont tendance à garder leur écorce plus longtemps, ce qui influence positivement le taux de survie des larves ou la condition physique des survivants en

atténuant les variations de température et les pertes d'eau des tissus sous l'écorce (Chararas 1981, Hanks et al. 2005). Pour un même degré de carbonisation, un arbre de plus fort diamètre contient également une plus forte abondance d'insectes saproxyliques puisqu'il possède une écorce plus épaisse qui protège les tissus sous l'écorce de la dessiccation en plus de posséder un phloème plus épais et nutritif pour les larves (Gardiner 1957, Saint-Germain et al. 2004a, Azeria et al. 2012). Ce facteur est toutefois moins important pour les espèces qui se nourrissent exclusivement de tissus sous-corticaux (Saint-Germain et al. 2004a). Dans certains cas, l'écorce plus épaisse des pins, comparativement aux épinettes, permet également de préserver plus efficacement l'humidité nécessaire aux insectes saproxyliques (Gardiner 1957, Saint-Germain et al. 2004b).

La sévérité du feu, la maturité et la composition des peuplements ainsi que le contexte spatial du paysage affectent la colonisation des brûlis et le développement larvaire des insectes saproxyliques (Saint-Germain et al. 2004a). Les insectes ne répondent toutefois pas tous de la même façon à ces facteurs et leur réponse dépend grandement de leurs exigences écologiques. Par exemple, une étude de Nappi et al. (2010) se déroulant 6 à 8 ans après le feu a montré que l'abondance des insectes de la famille des Scolytinae était plus grande dans les peuplements légèrement brûlés que sévèrement brûlés alors qu'il n'y avait pas de différence pour les Cerambycidae. Les Buprestidae étaient quant à eux maintenus en grands nombres dans les forêts sévèrement brûlées (Stepnisky 2003). Un facteur commun à toutes ces espèces est toutefois que leur présence dans les brûlis demeure éphémère. En effet, il ne peut y avoir qu'une seule génération de ces insectes puisque la structure et la valeur nutritive des tissus sous l'écorce se détériorent rapidement après la mort de l'arbre (Hanks 1999, Saint-Germain et al. 2004a).

De par leur dépendance aux insectes saproxyliques, les conditions générées par le feu influencent directement les pics qui s'en nourrissent. Par contre, l'occupation des forêts brûlées par les pics dépend également de leurs propres

techniques d'alimentation et leur préférence pour la nidification. En effet, le pic à dos noir creuse dans l'aubier des arbres à la recherche de larves de Cerambycidae et Buprestidae tandis que le pic à dos rayé écaille l'écorce des arbres pour accéder aux Scolytidae (Murphy et Lehnhausen 1998). Ainsi, le pic à dos noir a tendance à sélectionner les arbres moyennement à sévèrement carbonisés pour s'alimenter alors que le pic à dos rayé favorise les arbres légèrement carbonisés (Hannon et Drapeau 2005). Les pics préfèrent tous deux l'épinette noire au pin gris puisqu'elle possède une écorce plus mince qui permet d'accéder plus facilement à la nourriture (Farrar 1995, Hoyt et Hannon 2002). Par contre, la présence de pin gris dans un peuplement peut prolonger la disponibilité de nourriture puisqu'il prend généralement plus de temps à mourir que l'épinette (Hoyt et Hannon 2002). De plus, les pics préfèrent des arbres de fort diamètre qui contiennent généralement une plus grande abondance et richesse d'insectes saproxyliques (Nappi et al. 2003, Azeria et al. 2012). Les arbres de fort diamètre sont également recherchés pour la nidification des pics. En effet, ces arbres offrent la possibilité d'excaver de plus grandes cavités ayant des murs protecteurs et isolants plus épais (Schepps et al. 1999). Nappi (2009) a d'ailleurs constaté que les arbres ayant un diamètre de plus de 10 cm à la hauteur de poitrine (DHP) étaient particulièrement importants pour l'alimentation du pic à dos noir alors que ceux de plus de 20 cm de DHP étaient nécessaires pour la nidification. Sur d'autres aspects, les préférences pour l'alimentation contrastent drastiquement avec celles pour la nidification. Par exemple, les arbres déjà morts ou mourants avant le feu sont sélectionnés préférablement aux arbres tués par le feu pour la nidification, car ils sont souvent atteints de caries qui les rendent plus faciles à excaver (Nappi et Drapeau 2011).

Comme il a été vu pour les pics, la sélection d'habitats chez les oiseaux peut se faire à différents niveaux selon leurs besoins respectifs pour l'alimentation et la nidification. Des traits propres à chaque espèce tels que l'endroit et le type de nid fabriqué, et la technique d'alimentation peuvent servir d'indicateur approximatif de la

réponse des espèces au feu (Azeria et al. 2011). Dans une étude menée dans la pessière à mousse de l'Ouest du nord-ouest du Québec, Azeria et al. (2011) a montré que les insectivores sur l'écorce et le feuillage requièrent de grandes quantités d'arbres résiduels légèrement carbonisés, mais qu'ils préfèrent des peuplements contenant différentes essences selon leur guilde d'alimentation. Cette tendance a également été observée chez les nicheurs dans la canopée. Au contraire, les oiseaux se nourrissant ou nichant sol ou nichant dans les arbustes sont associés à des peuplements sévèrement brûlés puisque les feux sévères exposent les insectes et les graines (Koivula et Schmiegelow 2007).

Il est indéniable que la sévérité du feu et les conditions de la forêt avant le feu influencent fortement la réponse après feu des espèces (Schmiegelow et al. 2006). Il ne faut toutefois pas négliger un dernier aspect qui est le temps écoulé depuis le feu (Smucker et al. 2005). Les espèces qui obtiennent leurs proies du bois mort, telles que le pic à dos noir et le pic à dos rayé, colonisent rapidement les habitats brûlés. Puis, leur population décroit graduellement au fil des années suivant le déclin des insectes saproxyliques (Werner et Post 1985, Murphy et Lehnhausen 1998, Nappi et Drapeau 2009) qui peut prendre plus ou moins de temps selon la sévérité du feu. La présence de pic à dos noir dans une forêt sévèrement brûlée, par exemple, devient pratiquement nulle trois ans après le feu (Nappi et Drapeau 2009) alors qu'il peut encore être abondant 6 à 8 ans après le feu lorsqu'elle est légèrement brûlée (Nappi et al. 2010). Les granivores tirant avantage des graines tombées au sol tels que le tarin des pins (*Carduelis pinus*) et le bec-croisé des sapins (*Loxia cuurvirostra*) sont, eux aussi, plus abondants immédiatement après le feu. Leur population diminue ensuite rapidement, soit au courant de la seconde année alors qu'ils épuisent la disponibilité des graines (Hutto 1995). Les insectivores aériens, quant à eux, sont abondants autant dans les brûlis récents que dans les plus anciens (10 à 25 ans post-feu) (Bock et Lynch 1970) puisque le feu entraîne une diminution du couvert forestier et une augmentation d'arthropodes volants associés à la régénération des arbustes (Hobson et Schieck

1999). Différemment, les insectivores se nourrissant au sol deviennent de plus en plus abondants au fil des années puisque les arthropodes associés à la régénération de la forêt deviennent eux aussi plus nombreux (Saab et al. 2007). Cette raison explique pourquoi le pic flamboyant (*Colaptes auratus*) n'entre dans le système que trois ans après le feu malgré qu'il soit un excavateur primaire (Smucker et al. 2005). À plus long terme, l'assemblage des espèces continu à changer au fur et à mesure que les arbres morts tombent et la forêt se régénère pour laisser place à des espèces associées aux strates arbustives (Imbeau et al. 1999, Smucker et al. 2005, Schieck et Song 2006).

*Impacts de la coupe de récupération sur l'écosystème*

Bien que les feux de forêt jouent un rôle important dans le maintien de la biodiversité forestière, ils sont aussi en compétition directe avec les compagnies forestières puisqu'ils ont des répercussions sur la possibilité annuelle de coupe et conséquemment l'économie (Bergeron et al. 2004). La coupe de récupération, soit la récolte d'arbres morts ou mourants après une perturbation naturelle (Lindenmayer et Noss 2006), a donc été introduite comme moyen de minimiser les pertes économiques liées aux feux de forêts à grande échelle (Cahall et Hayes 2009). La coupe de récupération d'arbres brûlés est possible car le feu n'altère que les surfaces exposées de l'arbre étant donné que le bois possède une faible diffusivité thermique. La partie carbonisée de l'arbre peut donc être enlevée grâce à un écorçage agressif (Saint-Germain et Greene 2009). La récolte est toutefois contrainte à une courte période de temps suivant le feu car les champignons et les insectes saproxyliques dégradent rapidement le bois. De plus, la teneur en eau du bois diminue rapidement ce qui dévalue la pâte à papier. La coupe de récupération se fait donc habituellement dans les deux premières années suivant le feu (Saint-Germain et Greene 2009).

La coupe de récupération est répandue en forêt boréale de l'Amérique du Nord ainsi que dans d'autres écosystèmes où le feu joue un rôle important

(Lindenmayer et al. 2004). Au Canada, les réglementations concernant la coupe de récupération relèvent de la compétence provinciale et varient donc considérablement entre les provinces (Saint-Germain et Greene 2009). Au Québec, l'article 60 de la Loi sur l'Aménagement Durable du Territoire Forestier spécifie qu'un plan d'aménagement spécial doit être préparé avec la participation de la table locale de gestion intégrée des ressources et du territoire concernée. Ce plan doit spécifier le volume de bois à récolter et les traitements sylvicoles à employer. Cette loi stipule également que le plan peut déroger aux normes d'aménagement forestier applicables aux forêts non brûlées, telles que la rétention de bandes riveraines et de séparateurs linéaires, et dépasser la possibilité annuelle de coupe pour limiter les pertes de bois (Gouvernement du Québec 2013). Les standards pour la protection de l'environnement sont donc peu développés, causant souvent de larges étendues continues coupées sans rétention de bois brûlé sur pied (Nappi et al. 2011).

La pratique répandue de la coupe de récupération suscite des inquiétudes quant à ses impacts sur les écosystèmes et la diversité biologique puisque plusieurs espèces végétales et animales dépendent des brûlis (Nappi et al. 2004, Saint-Germain et Greene 2009, Lindenmayer et al. 2012). Les impacts de la coupe de récupération varient en fonction d'un large éventail de facteurs, tels que l'écosystème, les processus écologiques et les éléments du biote. À cela s'ajoute le type, la fréquence et le patron spatial de la coupe de récupération ainsi que les effets combinés de la perturbation naturelle et des opérations forestières (Lindenmayer et Noss 2006). Les impacts de la coupe de récupération peuvent être subdivisés en trois catégories, soient les impacts sur la structure des peuplements forestiers, sur les éléments particuliers du biote et l'assemblage des espèces, et sur les processus clés des écosystèmes (ex.: sur le cycle des nutriments). Ces effets peuvent également être étroitement liés ou cumulatifs (Lindenmayer et Noss 2006).

Les perturbations naturelles génèrent des legs biologiques particuliers tels que des arbres vivants et morts de forts diamètres, du bois mort au sol et des parcelles de forêt pas ou partiellement perturbées (Lindenmayer et Noss 2006). Le prélèvement de ces legs biologiques a pour effet d'homogénéiser le paysage (Radeloff et al. 2000), ce qui peut entraîner une simplification de la structure des peuplements (Hutto 1995). Les forêts ayant fait l'objet de coupe de récupération ont notamment une végétation de sous-bois moins riche, moins diversifiée et moins abondante que les forêts brûlées non perturbées (Purdon et al. 2004). De plus, le prélèvement de grandes quantités de legs biologiques peut être suivi par une longue période de temps avant que de nouveaux legs soient créés (Lindenmayer et Noss 2006). Par exemple, la récolte du bois mort sur pied empêche le recrutement de bois mort au sol pour une longue période de temps (Minshall 2003, Lindenmayer et Noss 2006). Dans un même ordre d'idée, la récolte vise avant tout les peuplements matures et productifs, laissant souvent des forêts résiduelles composées de peuplements immatures ou improductifs tels que les tourbières ou les dénudés secs (Nappi et al. 2011). Certaines classes de sévérité du feu peuvent également être préférées à d'autres alors que certains peuplements seront, quant à eux, épargnés par contraintes opérationnelles. Les peuplements résiduels ne sont donc pas représentatifs de ceux présents avant les opérations forestières (Nappi et al. 2011).

La coupe de récupération peut également avoir des impacts sur les peuplements par des moyens autres que la modification de la structure des peuplements (Lindenmayer et Noss 2006). Les semis qui germent rapidement après le feu peuvent, entre autres, être endommagés ou tués par le passage de la machinerie (Van Nieuwstadt et al. 2001). De plus, la machinerie peut dégrader la qualité des lits de germination ou même éliminer les semenciers (Noel 2001, Purdon et al. 2002, Greene et al. 2006). L'élimination des arbres a également pour effet d'augmenter la pénétration de la lumière jusqu'au sol forestier ou d'altérer le microclimat forestier, deux facteurs qui mènent à l'assèchement des sols. Cet assèchement entraîne une plus

faible régénération de certaines espèces nécessitant des milieux plus humides, tel que l'épinette noire, au détriment d'espèces associées à des conditions plus xériques (Noel 2001, Purdon et al. 2004, Greene et al. 2006). Finalement, le retrait rapide des épinettes noires et des pins gris, des essences possédant des cônes semi-sérotineux et sérotineux respectivement (s'ouvrant avec la chaleur), peut nuire au processus de régénération des peuplements et favoriser des essences non affectées par cette pratique comme le peuplier faux-tremble (Noel 2001, Greene et al. 2006, Boucher et al. 2014).

La perte de legs biologiques a, comme il a été mentionné précédemment, des conséquences sur les organismes dépendant de ces derniers (Hutto 1995, Saab et Dudley 1998, Morissette et al. 2002, Hutto 2006). La coupe de récupération altère donc substantiellement les assemblages d'espèces et les communautés nécessitant le bois brûlé sur pied dans les brûlis (Morissette et al. 2002). Par rapport à la forêt verte, la récolte de bois mort entraine des changements dans les communautés aviaires plus marqués que les feux non-récupérés (Morissette et al. 2002). En effet, l'abondance des espèces résidentes, insectivores et nichant dans les cavités et dans la canopée est réduite (Hutto 1995, Kotliar et al. 2002, Morissette et al. 2002). La communauté est plutôt composée d'espèces moins sensibles telles que des généralistes et des omnivores ainsi que d'espèces nichant au sol et dans les arbustes (Morissette et al. 2002, Cahall et Hayes 2009, Castro et al. 2010). Globalement, la récolte de bois mort entraîne une baisse de l'abondance et de la diversité aviaire d'environ 50% et 40% respectivement (Castro et al. 2010). Les autres taxons affectés par la coupe de récupération incluent les mammifères carnivores (Bull et al. 2001), les coléoptères hautement spécialisés (Buddle et al. 2000, Grove 2002), et les bryophytes (Scott 1985).

Finalement, la coupe de récupération peut avoir des répercussions sur divers processus clés des écosystèmes. La récolte a notamment des impacts sur les régimes

hydrologiques, la formation du sol forestier et le cycle des nutriments (Lindenmayer et Noss 2006) ainsi que sur les chaînes trophiques proies-prédateurs (Nappi et al. 2011). La récupération du bois mort à l'aide de machinerie lourde ainsi que la construction de routes a pour effet de compacter le sol, d'enlever une partie de la matière organique et d'augmenter la quantité et la durée de l'érosion et du ruissellement de la terre végétale (« topsoil ») (McIver et Starr 2000). Éliminer le bois mort, qui retient normalement les sédiments, engendre une augmentation de la magnitude des débits érosifs et des charges sédimentaires, ce qui modifie les caractéristiques des canaux fluviaux et nuit à une grande quantité d'espèces aquatiques allant des invertébrés jusqu'aux poissons (Minshall 2003). Les effets de la coupe de récupération sont d'autant plus graves si elle a lieu sur des pentes abruptes, des sols sensibles à l'érosion, des sites sévèrement brûlés ou près des berges (Karr et al. 2004). Par exemple, récupérer le bois mort sur les berges dégrade l'environnement aquatique en élevant la température de l'eau, altérant l'hydrologie, augmentant la sédimentation et diminuant l'apport de bois mort dans les cours d'eau pouvant servir de sites de frai pour certaines espèces aquatiques (Karr et al. 2004). Une étude se déroulant au Québec a, quant à elle, démontré que la récolte des bois sur des sites sévèrement brûlés a mené à une perte de calcium, de magnésium et de phosphore à des niveaux qui ne pourront pas revenir d'ici la prochaine rotation forestière (Brais et al. 2000). Tous ces exemples, quoique non exhaustifs, démontrent que la coupe de récupération à des impacts négatifs sur plusieurs aspects des écosystèmes et qu'ils devraient être pris en considération lors de l'élaboration des plans d'aménagement spéciaux des forêts brûlées.

*La rétention de bois mort maintient-elle efficacement la biodiversité?*

Des études récentes ont démontré que la rétention d'arbres morts ou de peuplements brûlés dans les parterres de coupe de récupération peut en atténuer les effets négatifs sur les écosystèmes et maintenir quelques espèces associées aux arbres

morts (Saab et Dudley 1998, Haggard et Gaines 2001, Schwab et al. 2006). La rétention de bois mort permet, entre autres, d'améliorer les conditions environnementales ainsi que les propriétés du sol (ex : rétention d'eau et d'éléments nutritifs), favorisant ainsi la régénération naturelle et la productivité des sites (Brais et al. 2000, Purdon et al. 2002). Les principaux types de rétention testés incluent des coupes partielles visant à maintenir un certain nombre de tiges par hectare de façon isolée ou en groupe (Saab et Dudley 1998, Haggard et Gaines 2001) ainsi que des îlots de tailles variables (Hutto et Gallo 2006, Schwab et al. 2006). De façon générale, moins l'intensité de la coupe est importante, plus le couvert forestier et la structure hétérogène des peuplements nécessaires à la faune sont préservés, affectant positivement les espèces associées aux brûlis (Saint-Germain et Greene 2009). Les seuils minimaux de rétention permettant de maintenir un maximum d'espèces associées aux habitats post-feux diffèrent toutefois d'une étude à l'autre. Cela pourrait s'expliquer par la grande variabilité des peuplements brûlés ainsi que par les espèces présentes sur le site d'étude. En effet, certaines espèces préfèrent des habitats ouverts alors que d'autres requièrent une plus grande densité d'arbres. À ma connaissance, peu d'études tiennent compte à la fois du type de rétention et des conditions pré- et post-feu des peuplements pour déterminer les meilleures stratégies de rétention à adopter. Plusieurs études se concentrent sur un sous-ensemble de conditions générées par le feu afin de limiter la variabilité des résultats. Or, pour offrir des solutions d'aménagement qui conviennent à un plus large spectre de conditions, il importe de les intégrer dans les études. La présente étude vise donc à déterminer les facteurs générés par le feu ainsi que les types de rétention à privilégier pour maximiser le maintien des espèces associées au bois mort dans les forêts brûlées récupérées.

*Objectifs et structure du mémoire*

Les objectifs de cette étude sont de caractériser les communautés aviaires dans différents types de rétention contenant un large spectre de conditions pré- et post-feu et de déterminer les impacts de la coupe de récupération sur cette communauté. Le but ultime est de fournir des solutions d'aménagement de la forêt brûlée qui combinent l'activité de récolte de bois (coupe de récupération) à une rétention du bois brûlée favorable au maintien de la diversité biologique (par le biais des espèces associées à cet habitat). Ce mémoire comprend un chapitre rédigé sous forme d'article qui contient trois sous-objectifs.

Dans un premier temps l'accent est mis sur une présentation d'ensemble de la variation de la communauté aviaire en fonction de la stratégie de rétention utilisée dans un feu qui a fait l'objet d'un plan de récupération des bois brûlés. Puis, l'étude cherche à identifier de façon plus spécifique les facteurs écologiques à de multiples échelles spatiales (échelle locale, de la parcelle et du paysage) qui affectent la distribution de neuf espèces associées au bois mort (8 cavicoles – 1 corticole) dans les habitats brûlés résiduels. Enfin, comme la présence des oiseaux en période de reproduction n'est pas nécessairement un indicateur adéquat de leur capacité à se reproduire avec succès (un indicateur plus adéquat de la qualité d'habitat), l'étude a pour troisième objectif de déterminer la présence de cavités excavées par les trois espèces de pics (pic à dos noir, pic à dos rayé et pic flamboyant) les plus susceptibles d'utiliser la forêt brûlée résiduelle afin de vérifier comment les divers types de rétention affectent la persistance des populations de ces espèces dans le brûlis aménagé.

CHAPITRE I

# HOW CAN SNAG RETENTION STRATEGIES MAINTAIN POST-FIRE BIRD SPECIES IN RECENT BURNS ?

Chantal Cloutier [1] and Pierre Drapeau [1]

[1] Université du Québec à Montréal, Département des sciences biologiques, Centre d'Étude de la Forêt (CEF), Chaire industrielle CRSNG UQAT-UQAM en aménagement forestier durable.

## *1.1 Abstract*

Burned forests represent quality habitat for many species associated with deadwood. Yet, post-fire salvage logging is becoming more prevalent as forest companies try to recover some of the economic losses caused by fire. Several snag retention strategies have therefore been proposed to minimize the negative impacts of this practice on biodiversity. However, their efficiency to maintain biodiversity is poorly documented. The efficiency of three types of retention strategies (i.e. isolated stems, riparian strips and patches of variable size) was assessed in a partially salvaged burn located 250 km north of Lac-Saint-Jean, Quebec, using the post-fire bird community as a biological indicator. Fixed-radius point-counts and playbacks were used to detect birds in 71 stations that covered a gradient of fire severity, forest maturity and tree species composition. Nesting-cavities of three primary excavators (the Black-backed Woodpecker, American Three-toed Woodpecker and Northern Flicker) were also located by systematic searching along four transects at each station. Community analysis revealed that isolated stems and riparian strips were less efficient at maintaining deadwood-associated species such as primary and secondary cavity-nesters than patches greater than 20 ha. Hierarchical generalized linear modeling of the occurrence of cavity-nesters revealed that the density of black spruce trees and the area of unsalvaged burned forest within a 250 m-radius were the two main variables affecting their distribution. The presence of moderately to severely charred trees as well as the area of unsalvaged burned mature forest in the landscape influenced the nest site selection of Black-backed Woodpeckers, the most significant provider of cavities in our system. In addition, the maintenance of a deciduous component within coniferous stands allowed Northern Flicker to nest, regardless of the size of the retention. In light of these results, we suggest to favour the retention of patches greater than 20 ha containing a high density of burned mature trees that cover a gradient of fire severity. Deciduous trees should also be retained, most importantly when retaining isolated stems to provide nesting substrates for the Northern Flicker.

**Key words:** fire, salvage logging, cavity-nester, bark-nester, snag retentions

Résumé

Les forêts brûlées constituent un habitat de qualité pour plusieurs espèces associées au bois mort. Pourtant, ces brûlis sont de plus en plus convoités pour la récolte de bois afin de minimiser les pertes économiques reliées aux feux. La rétention de parcelles brûlées a donc été proposée pour mitiger les effets négatifs de cette pratique sur la biodiversité. Leur efficacité à maintenir cette dernière est toutefois peu documentée. L'efficacité de trois types de rétention (c.-à-d. des tiges isolées, bandes riveraines et parcelles de taille variable) a été testée dans un brûlis partiellement récupéré situé à 250 km au nord du Lac-Saint-Jean, Québec, en utilisant la communauté aviaire post-feu comme indicateur biologique. Des points d'écoute à rayon fixe et des repasses de chant ont été utilisés pour détecter les oiseaux dans 71 stations couvrant un gradient de sévérité du feu, de maturité et de composition en essences d'arbres. À chaque station, les cavités excavées par trois espèces cavicoles primaires (le pic à dos noir, pic à dos rayé et pic flamboyant) ont aussi été cherchées systématiquement le long de quatre transects. Une analyse de communautés a montré que les tiges isolées et les bandes riveraines ne maintenaient pas aussi efficacement les espèces associées au bois mort telles que les espèces cavicoles primaires et secondaires que les parcelles de plus de 20 ha. Des modèles linéaires généralisés hiérarchiques sur l'occurrence des espèces cavicoles ont révélé que la densité d'épinettes noires et la superficie de forêt brûlée non-récoltée à l'intérieur d'un rayon de 250 m étaient les principales variables influençant leur distribution. La présence d'arbres moyennement à sévèrement carbonisés ainsi que la superficie de forêt brûlée mature dans le paysage influençaient également la sélection de sites de nidification du pic à dos noir, l'excavateur principal de cavités dans notre aire d'étude. De plus, la présence d'essences décidues comme le bouleau à papier permettait au pic flamboyant de nicher et ce, peu importe la taille de la rétention. À la lumière de ces résultats, nous suggérons de maintenir une variété de types de rétention tout en favorisant les parcelles de plus de 20 ha contenant une forte densité d'arbres brûlés matures couvrant un gradient de sévérité du feu. Les essences décidues devraient également être maintenues, surtout dans les rétentions de tiges isolées, puisqu'elles peuvent servir de substrat de nidification pour le pic flamboyant.

**Mots clés:** feu, coupe de récupération, espèce cavicole, espèce corticole, rétention de bois mort

## *1.2 Introduction*

Post-fire salvage logging (the removal of dead or dying trees after a natural disturbance; Lindenmayer and Noss 2006) has been increasingly used in the boreal forest of North America as well as in other ecosystems where fire plays a predominant role (Lindenmayer et al. 2004). Economic reasons, such as partially recovering timber values, are often cited to justify salvage logging (McIver and Starr 2000). In many jurisdictions, management plans for recent burns can derogate from forest management standards prescribed for unburned forests such as the retention of linear and riparian buffer strips (Saint-Germain and Greene 2009). This lack of regulation reduces the protection of the environment, often causing large expanses of forests to be completely salvage-logged (Nappi et al. 2011). There is now growing evidence that this practice has negative repercussions on ecosystem structure and function. In fact, it affects nutrient cycling, watershed runoff and erosion, vegetation regeneration and animal and plant diversity (McIver and Starr 2000, Morissette et al. 2002, Karr et al. 2004, Lindenmayer and Noss 2006). These findings prompted the urgency of developing more sustainable management guidelines for recent burns (Hutto 2006).

Bird biotic responses to salvage logging have been investigated in many studies to develop sustainable management guidelines (Kotliar et al. 2002, Morissette et al. 2002, Hutto 2006) since birds are considered as good indicators of ecological integrity of forest habitats (Mikusiński et al. 2001). Forest fires generate structural and compositional habitat heterogeneity that results in a reorganization of bird communities (Smith 2000). The resulting habitat, characterized by large numbers of snags, favors cavity- and canopy-nesting birds (Hutto 1995, Saab and Dudley 1998, Kotliar et al. 2002), aerial insectivores (Hutto 1995, Kotliar et al. 2002) and ground- and shrub- foraging birds (Bock and Lynch 1970). Recent burns are particularly important for primary cavity-nesters (i.e. woodpeckers) that are attracted to the

sudden availability of snags and insect prey (i.e. saproxylic insects: insects that are dependent on dead wood to complete at least one stage of their life cycle; Saint-Germain et al. 2007) (Hoyt and Hannon 2002, Nappi et al. 2003, Koivula and Schmiegelow 2007). In turn, woodpeckers excavate cavities that are subsequently used by many bird and mammal secondary cavity-nesting species (Martin et al. 2004), a concept known as "nest web" (Bednarz et al. 2004, Martin et al. 2004). Hence, woodpeckers become keystone species in burned habitats by providing resources that facilitate the survival and viability of many forest organisms that are dependant on tree cavities (Saab et al. 2004). Woodpecker populations nevertheless depend substantially on the forest landscape structure and individual tree characteristics in burns (Saab et al. 2004), making them and secondary cavity-nesters vulnerable to salvage logging. Post-fire harvesting thus not only affects the taxonomic but also the functional diversity that characterizes the complex ecological network of organisms that rely on decaying and dead trees in recent burns.

Intensive salvage logging that removes all or nearly all snags from an area homogenizes the landscape (Radeloff et al. 2000) and simplifies the forest structure (Hutto 1995), which consequently alters post-fire bird communities. In fact, this practice creates conducive conditions for generalist and omnivore species as well as species adapted to open-canopies such as ground- and shrub-nesters (Morissette et al. 2002, Cahall and Hayes 2009, Castro et al. 2010). Few studies have investigated the impacts of partial harversting in burns, which consists in retaining a predetermined density of snags or patches of variables sizes, on bird biotic responses (Saab and Dudley 1998, Haggard and Gaines 2001, Schwab et al. 2006). Results indicate that although bird responses are species-dependent and vary according to the management strategy, partial harvesting has the potential to mitigate some of the negative impacts of salvage logging (Saab and Dudley 1998, Haggard and Gaines 2001, Schwab et al. 2006). A better understanding of the impacts of partial post-fire harvesting on bird

communities as well as the habitat requirements of species associated to burned forests is, however, still needed to develop better management strategies.

During the summer of 2010, a fire burned 33 000 hectares of boreal forest in the northern region of Lac-Saint-Jean, Quebec. The burned landscape included a mixture of burn severity, forest maturity and tree species composition. The special management plan put in place retained 29 % of the area using different snag retention strategies. This salvage-logged forest provided us an opportunity to deepen our knowledge of the impacts of partial harvesting on bird communities. To investigate bird responses to partial harvesting, we developed a study design that had three objectives. First, we investigated how the bird community as a whole responded to different retention strategies to determine which one worked best at maintaining deadwood-associated species. Since cavity-nesters are sensitive to salvage logging but also to other factors (such as fire severity, pre-fire forest conditions) that may interact with salvage logging, we also modeled their habitat requirements at the local, patch and landscape scales by incorporating these factors as covariables. Finally, we analysed the presence of cavities excavated by three primary cavity-nesters, the Black-backed Woodpecker (*Picoides articus*), American Three-toed Woodpecker (*Picoides dorsalis*), and Northern Flicker (*Colaptes auratus*), to determine which factors affect their nest site selection and consequently are most likely to sustain the nest web.

## *1.3 Methods*

### 1.3.1 Study site

The study was conducted in the western black spruce-moss bioclimatic domain of Quebec, Canada (Saucier et al. 2011). This domain is composed of 90 % pure black spruce (*Picea mariana*) stands (Boucher et al. 2003). Fire is the main natural disturbance in the region with a current fire cycle (1734 - 2009) estimated at

247 years (Bélisle et al. 2011). The study area is located 250 km north of Lac-St-Jean, between 50°37' and 50°52'N and 71°30' and 71°51'W. A 33 000 ha wildfire (Fire # 433) occurred from June 19th to July 9th, 2010. The fire was highly variable in fire severity as defined by aerial photos. In fact, 5 % of the forested area was unburned, 23 % lightly, 40 % moderately and 32 % severely burned. The original forest cover also varied in maturity as a portion of the affected area had previously burned 30 years ago. The original forest cover was mainly composed of mature (>12 m high) black spruce trees (55 % of the forested area) and immature (between 7 and 12 m high) black spruce trees (12 %). The second most abundant species was jack pine (*Pinus banksiana*) (1 % mature and 2 % immature). Other tree species included balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*) and tamarack (*Larix laricina*) (Table 1.1 summarizes this information).

Resolute Forest Products, the company responsible for this forest management unit, in collaboration with the Ministry of Natural Resources and Wildlife of Quebec developed a management plan that retained 29 % of the burned forest (Figure 1.1). They began salvage logging operations on July 12th, 2010 and completed them by February 2011. No salvage logging occurred in protected areas and biological refuges as well as in unburned patches greater than 2 ha or within 20 m of any watercourse. The latter type of retention, which will hereafter be called riparian strip, represented approximately 7 % of the total retention. The remaining unsalvaged forest was left either as patches of different shapes and sizes or as isolated stems (minimum of 10 merchantable stems per hectare). Of the unsalvaged area, 53 % was lightly, 25 % moderately and 21 % severely burned. Finally, 8 % and 19 % of the immature and mature black spruce trees, and 1 % and 1 % of the immature and mature jack pine trees were retained respectively.

### 1.3.2 Study design

The retained burned stands can be described with three characteristics: forest maturity, burn severity and type of retention. The types of retention included isolated stems, riparian strips and patches. However, patches varied greatly from one to another (their size ranged from less than a hectare to over 3000 ha). We subdivided them into three size classes: patches smaller than 20 ha, between 20 and 150 ha and greater than 150 ha. The rationale is that the home range of the keystone cavity-producing species in post-fire stands, the Black-backed Woodpecker, covers an area of 20 ha in severely burned stands (Nappi 2009) whereas its mean home range reaches 151.5 ha in unburned boreal forest of our study region (Tremblay et al. 2009). Since fire severity at the study site varied between light to severe, a patch greater than 20 ha should be adequate to accommodate a Black-backed Woodpecker in a severely burned stand whereas a patch greater than 150 ha should be sufficient in a lightly burned stand.

Site selection aimed at choosing the maximum number of combinations of forest maturity, fire severity and type of retention. It was, however, not possible to obtain all combinations as some were inexistent or inaccessible due to road degradation. The protected areas and biological refuges, which could have served as references, were not accessible either. The results of the study nevertheless provide insights on which management strategies worked best at maintaining cavity-nesting species in the salvage-logged system.

### 1.3.3 Bird sampling

Bird counts were performed three years after the fire (2013) using two methods: point-counts and playbacks. Point-counts are suitable for bird species that are easily detectable by sound and sight whereas playbacks are appropriate for species that cannot be detected or identified easily (Bibby and Burgess 2000), such as

species of the Picinae subfamily which are inconspicuous and possess large home ranges (Bibby and Burgess 2000, Keller et al. 2003).

To perform bird counts, one station was established in each of the retentions selected beforehand for a total of 71 stations (8 isolated stems, 23 riparian strips, 12 patches smaller than 20 ha, 9 patches between 20 and 150 ha and 19 patches greater than 150 ha). Isolated stems covered, on average, an area of 1.1 $\pm$ 1.0 S.E. ha, riparian strips 34.9 $\pm$ 20.2 S.E. ha, patches smaller than 20 ha 7.6 $\pm$ 1.6 S.E. ha, patches between 20 and 150 ha 60.1 $\pm$ 13.7 S.E. ha and patches greater than 150 ha 878.1 $\pm$ 148.1 S.E. ha. Sampling stations were separated by a minimum of 625 m (1178.0 $\pm$ 52.5 m S.E.) which is considered as sufficient to avoid double counts of individuals and thus ensure the independence of counts. In fact, this distance is greater than the 200 m suggested by Martin et al. (1997) because many of the species of interest, such as woodpeckers, have large home ranges (Bibby and Burgess 2000). In riparian strips or isolated stems, the stations were established in the middle of the retention to maximize the area of retention covered by the census. In patches, the stations were located at least 75 m from the edge to avoid recording species outside the patch. An edge was defined as a boundary between a forest stand and a salvaged area, a road or a body of water.

At each point-count, the number of individuals of each forest bird species detected by sound or sight within a 75 m-radius was recorded during three consecutive periods of 5 minutes for a total of 15 minutes per visit. A fixed radius was used to ensure that the individuals recorded were associated with the type of retention of interest. Each site was visited three times during the breeding season (from late-May to early-July) between 4:00 and 9:00 in the morning, when birds were most active (Bibby and Burgess 2000). Point-counts were postponed when winds were exceeding 8 km/h or when it was raining because it reduced the observers' capacity of detection (Bibby and Burgess 2000, Drapeau et al. 2000). Three different

observers were involved in point-counts. To minimize bias and ensure comparability of counts between observers and stations, we rotated observers and trained them prior to the field season.

Two playback visits, usually held on different days than point-counts, were performed during the breeding season. A total of eight cavity- and one bark-nesting species associated with burned forests were chosen: the Black-backed Woodpecker (*Picoides articus*), American Three-toed Woodpecker (*Picoides dorsalis*), Northern Flicker (*Colaptes auratus*), Tree Swallow (*Tachycineta bicolor*), Red-breasted Nuthatch (*Sitta canadensis*), Eastern Bluebird (*Sialia sialis*), Boreal Chickadee (*Parus hudsonicus*), American Kestrel (*Falco sparvarius*) and Brown Creeper (*Certhia americana*), the bark-nester. Although all these species can be found in burned forests, they possess different affinities with burns (Imbeau et al. 1999, Drapeau et al. 2010). Furthermore, they are present at different time periods after the fire. Some of these species are also more sensitive to salvage logging than others (Morissette et al. 2002) (see Table 1.2 for further details).

A FoxPro device was used to emit the songs and calls of the nine cavity- and bark-nesting species. The volume was set to reach a distance of 75 m in burned forests. Each species, with the exception of woodpeckers, was called for a minute followed by 30 seconds of silence to hear the bird response. Woodpeckers were called for two minutes followed by one minute of silence because it increases their rate of response (Ibarzabal and Desmeules 2006).

### 1.3.4 Nest search

The effects of salvage logging on woodpecker's breeding activity were evaluated by comparing the environment of a site containing at least one nesting cavity (used or unused) to a site without one. To do so, we searched for Black-backed Woodpecker, American Three-toed Woodpecker and Northern Flicker nests during

the breeding season of 2013 (late-May to early-July). Black-backed and American Three-toed Woodpeckers, two boreal woodpeckers, were chosen because they both positively respond to forest fires (Hutto 1995, Murphy and Lehnhausen 1998, Nappi and Drapeau 2009) and are sensitive to salvage logging (Haggard and Gaines 2001, Hutto 2006, Hutto and Gallo 2006, Cahall and Hayes 2009). The Northern Flicker, although less sensitive to salvage logging, was chosen because it represents a keystone species in western boreal forests and could play a similar role within our study area. Indeed, this ground-insectivore excavates larger cavities than boreal woodpeckers that can be used by a greater diversity of secondary cavity-nesters (Martin et al. 2004).

At each station, nesting cavities were located by systematic searching along four 300 m-long transects separated by 100 m. These transects covered a 300 m x 300 m grid. If a portion of the grid fell into a completely salvaged area, it was not surveyed. Nest searching efforts were nevertheless standardized. All transects were walked three times during morning hours (4h30 – 12h00) in different directions to maximize the odds of finding a cavity. Cavities were located by following adults, listening for nest excavation or begging nestlings. Furthermore, 2 min-playbacks of each species, which covered a 150 m-radius, were used midway along the four outer edges of the grids to increase their detection (Resources Inventory Committee 1999). Some cavities were found opportunistically outside the grids and were added to the analyses. Geographic coordinates of the cavities were recorded in a GPS to retrieve them subsequently. Characteristics of the tree, cavity and development stage of the brood were taken with the help of a telescopic camera. Cavity characteristics such as the entrance shape and size allowed us to identify the primary excavator when the cavity was unoccupied or used by a secondary cavity-nester (Dudley and Saab 2003). Identifying the primary cavity-nester of Northern Flicker cavities can be tricky because they are weak excavators and sometimes reuse cavities excavated by other

cavity-nesters (Aitken et al. 2002). However, it is more likely that they excavated their own cavities in our study area as trees deteriorated by fire are easier to excavate.

Finally, all nesting cavities (used or unused) were considered since they were excavated after the burn was salvage logged. Indeed, by the time the fire was extinguished, the woodpecker breeding season was over and logging operations were completed before the next breeding season. Therefore, we are confident that these cavities were excavated after salvage logging operations were completed.

### 1.3.5 Local vegetation sampling

Local vegetation was characterized using a 11.28 m-radius vegetation plots centered on each station. Within each plot, we recorded diameter at breast height (DBH) and species for each tree having a DBH ≥10 cm. We also described each of these trees using three characteristics: the degradation stage (Imbeau and Desrochers 2002), trunk charring and bark loss (Nappi et al. 2010). The degradation stage described the general condition of the tree (1: ≥ 95 % of the foliage intact, 2: 20 to 95 % of foliage intact, 3: < 20 % intact foliage; senescent, 4: recently dead tree to 7: standing stump < 2 m tall). Trunk charring referred to the trunk surface that was burned (1: 0 %, 2: 1-40 %, 3: 41-95 % and 4: 96-100 %). Finally, bark loss referred to the proportion of bark lost on the trunk surface (1: 1-25 %, 2: 26-50 %, 3: 51-75 % and 4: 76-100 %). In addition to the vegetation sampling, the fire severity (unburned: all trees are green, lightly: > 50 % of the trees are green, moderately: < 50 % of the trees are green or the needles are scorched, severely: all trees are burned; Ressources naturelles et Faunes Québec 2012) and maturity (immature: 7-12 m, mature: ≥ 12 m) of the stands were characterized within a 75 m-radius centered on each station.

Fire severity at the stand scale, as estimated in the field, partly reflected the effect of fire on tree degradation and trunk charring at the tree scale (Kruskal-Wallis test $p < 0.01$) (Table 1.3). Proportion of live and declining trees tended to decrease

with increasing fire severity whereas dead trees tended to increase. Trunk charring at the tree scale tended to increase with increasing fire severity. Conversely, fire severity did not reflect significantly bark loss at the tree scale. However, the proportion of trees that retained their bark tended to decrease with increasing fire severity (Table 1.3). Given these mixed results at the tree scale, fire severity at the stand level was used in further analyses instead of the three tree characteristics.

Vegetation plots (11.28 m-radius) were also used to characterize the environment chosen by breeding woodpeckers. However, three vegetation plots were used instead of one. One plot was centered on the cavity tree whereas the other two were placed at 50 m from the cavity in opposite directions. To assess if woodpeckers selected specific breeding environments, these measurements were compared to three vegetation plots sampled in a similar type of retention without any cavity.

### 1.3.6 Landscape variables

Landscape variables were obtained from aerial photos taken by the Ministry of Natural Resources of Quebec after the completion of salvage logging operations as well as from ecoforest maps provided by the Resolute Forest Products company. The ecoforest maps provided information on burn severity, age and height of the stands as well as forestry activities (salvage logging, scarification and tree planting) that occurred during the three years following the fire. The ecoforest maps did not always reflect what was observed in the field. So they were first manually corrected by taking the post-treatments aerial photos as references using the Geographic Information System (GIS) ArcGIS10.1 (ESRI 2011). The resolution of these photos was of 30 cm x 30 cm which allowed precise delimitation of the retention areas. Once the corrections were completed, the landscape surrounding each station was characterized using two radii: 250 and 500 m. The landscape was first characterized by calculating the total area of unsalvaged burned forest (UBF). Since unsalvaged burned stands were composed of both immature and mature forests, we further

characterized the landscape by calculating the area of unsalvaged burned mature forest (≥ 12 m in height) (BM). The Euclidean distance between each station and the nearest unburned forest (DU) was also measured. Finally, the total unsalvaged burned area covered by each fire severity was tabulated in order to create a fire severity index (FSI) using the Simpson's diversity index. This index was used to describe how fire severity varied throughout each radius. Values, which varied between 0 and 1, represented the lowest and highest variability in fire severity respectively.

### 1.3.7 Data analyses

*Correspondence analysis of salvaged post-fire avian communities*

The bird species presence-absence data matrix was first analyzed by correspondence analysis (CA) in order to provide a visual representation of the sampling stations on a two axes dispersion diagram. This multivariate method places sites that are similar in species composition close to each other in an Euclidean space. CA was also used to compare the species composition of bird communities according to the type of retention. To do so, the rarest species were first removed from the analysis according to Legendre and Legendre's (2012) method because they contain a large number of zeros. These zeros contribute heavily to the chi-square distance, which is the distance preserved in this type of analysis (Legendre and Legendre 2012). The species present in only one or two sites out of 71 burned sites were thus removed from the analysis, leaving a total of 30 species. Then, 95 % confidence interval ellipses based on the standard error of the type of retention were overlaid on the diagrams. Variations in fire severity, stand maturity, tree species composition and area of unsalvaged burned forest represented by each type of retention were also tested by ANOVA and Tukey's Post Hoc tests (Table 1.4).

*Hierarchical generalized linear models of the cavity-nesting guild*

We used hierarchical generalized linear models (GLM) to identify the factors at the local, patch and landscape scales that affect the distribution of cavity- and bark-nesting species in the remaining burned stands of the fire. Hierarchical GLM models are well suited to account for interrelated environmental variables measured at different scales (Brotons et al. 2003). Variables at the local scale included the density (stems/ha) of black spruce (BLS), jack pine (JAP) and balsam fir (BAF) burned trees, the density of snags with a DBH smaller (DS10) and larger than 20 cm (DS20) and fire severity (FS). However, tree densities were first corrected to account for the area of unsalvaged burned forest within the 75 m-radius which varied from one sampling station to another and among retention types. To do so, tree densities were multiplied by the proportion of the 75 m-radius covered by unsalvaged burned forest. Patch scale included the five types of retention (isolated stems (IS), riparian strip (RS), patch < 20 ha (P0), patch between 20 and 150 ha (P20) and patch >150 ha (P150)). Finally, landscape variables included all variables collected by geomatic techniques within the 250 and 500m radii (total area of unsalvaged burned forests (UBF250 and UBF500), area of unsalvaged burned mature forest (BM250 and BM500), fire severity index (FSI250 and FSI500) and distance to the nearest unburned patch (DU)).

We first performed hierarchical generalized linear modelling to the species richness of cavity-and bark-nesting birds by combining point-count and playback data. Explanatory variables were allowed to enter in groups corresponding to their spatial scale (Model 1). We started with a null model that included no variable. The hierarchical approach included three steps. The first step included variables describing the local scale, the second included variables at the patch scale as well as their interactions with the variables at the local scale, and the third step included variables at the landscape scale and their interactions with variables at the patch scale.

At each step, we forced the inclusion of variables proven significant at the previous step before adding any additional variables. This method allowed us to measure the additional explanatory power of variables at each step after controlling for the effects of the variables at a finer scale. At each step, a forward selection of the variables was used to select the best explanatory factors of bird richness. The variables were first chosen based on their AIC and then by verifying that their confidence interval did not include zero.

We then developed a second model (Model 2) that did not include local variables. This model assessed the influence of patch and landscape variables on bird richness as well as their interactions. Finally, we developed a third model (Model 3) that only included variables at the landscape level. These models allowed us to assess the possible effect of intercorrelations between explanatory variables at different spatial scales on bird richness.

Since some of the cavity-nesting species chosen for this analysis are not sensitive to salvage-logging, the same analyses were performed by excluding these species from the total species richness (hereafter called species richness of sensitive cavity-nesters) to determine if they altered the results.

The same analyses were also performed at the individual species level. Just as for the species richness, the point-count and playback data were combined. However, the abundance of a species at a site was usually quite low (maximum of 2 individuals). For this reason, the data were first transformed into presence-absence and treated with binomial regression analysis. The final model selected after the three steps was the one with the lowest Akaike information criterion (AIC).

*Generalized linear mixed models of woodpeckers nest sites*

The third part of the analyses aimed at identifying the factors that influenced woodpecker nest site selection. When a cavity was found, vegetation measurements

were taken and compared to a similar type of retention without any cavity. For this reason, the data were analyzed using generalized linear mixed models which take into account the hierarchical structure of the sampling design. The group of six vegetation plots compared to each other was used as the random effect to ensure that differences between occupied and unoccupied sites were taken into account. We developed 6 *a priori* hypotheses that included factors that might influence nest site selection based on literature and our own field experience. Since we only found Black-backed Woodpecker and Northern Flicker nests, we developed hypotheses that were common or specific to each species (Table 1.5).

From the original 6 hypotheses, we generated a set of 8 candidate models for the Black-backed Woodpecker and 6 for the Northern Flicker. The candidate models included a null model, individual factors, additive factors and a global model. We modeled nest site selection as a binomial process, where a site was considered as used (1) or unused (0) for nesting.

The candidate models were compared and the most parsimonious one was selected using the theoretical-information approach which uses the Akaike information criterion adjusted for small sample size (AICc) (Burnham and Anderson 2002). Models having a ΔAICc smaller than 2.0 were considered as having strong support for the data (Burnham and Anderson 2002). Multi-model inference was performed for variables present in closely competing models (ΔAICc < 4.0). This was done by averaging estimates of the variables across models weighted by Akaike weights (Wi). These weights quantify the support of one model in comparison to other candidate models (Burnham and Anderson 2002).

### *1.4 Results*

In 71 sites, we recorded a total of 1166 individuals of 37 forest bird species by point-counts and 38 individuals of 6 species by playbacks. The total species richness

of the sites for both methods ranged from 2 to 15 (Mean ± S.E.: 7.6 ± 0.4 species). The two commonest species were the White-throated Sparrow (*Zonotrichia albicollis*) and the Dark-eyed Junco (*Junco hyemalis*) which had an occurrence of 96 and 94 % respectively (Figure 1.2). The number of cavity-nesters ranged from 0 to 3 (Mean ± S.E.: 1.1 ± 0.1 species). The commonest cavity-nester was the Tree Swallow with an occurrence of 48 % followed by the Black-backed Woodpecker with an occurrence of 37 %. The breakdown of the total species richness as well as the richness of cavity-nesting species for each type of retention can be found in Table 1.6.

### 1.4.1 Correspondence analysis of salvaged post-fire bird communities

The first two axes of the correspondence analysis (CA) summarized 18 % of the variation in species composition. The size of the ellipses on the first two axes representing the types of retention indicate that patches, irrespective of their size, possess a greater variation in bird species composition than riparian strips or isolated stems (Figure 1.3). However, patches between 20 and 150 ha are the ones that possess the greatest species variation. The position of the ellipses on the diagram illustrate a transition in bird species composition from isolated stems and riparian strips on the left to patches greater than 20 ha on the right of the horizontal axis (Figure 1.3). The amount of overlap shown by the ellipses also indicates a similarity in bird species composition between certain types of retention. For example, patches smaller than 20 ha share a higher proportion of their species composition with riparian and isolated tree retention types than with the two large patch retention types (Figure 1.3). Accordingly, the CA species ordination diagram shows a segregation of bird species associated with open habitats such as the Lincoln's Sparrow, American Robin, Dark-eyed Junco, Hermit Thrush, Palm Warbler and Tree Swallow on the left side of the ordination to species that require a greater density of burned trees such as the Black-backed Woodpecker, Three-toed Woodpecker, Winter Wren and Brown

Creeper on the right end of the axis (Figure 1.4). The second axis segregates early-successional and young forest species (such as Common Yellowthroat, Yellow Warbler and American Redstart) at the upper end of the diagram, and mature forest birds such as American Three-toed Woodpecker, Brown Creeper and Swainson's Thrush at the lower end (Figure 1.4).

### 1.4.2 Hierarchical generalized linear models of the cavity-nesting guild

The hierarchical generalized linear modeling aimed at identifying the factors affecting the distribution of cavity- and bark-nesting species in the unsalvaged burned stands at the local, patch and landscape scales. Out of the nine species surveyed, three species, the American Kestrel, Red-breasted Nuthatch and Boreal Chickadee, were never recorded. The Tree Swallow, Black-backed Woodpecker, Brown Creeper, Eastern Bluebird and Northern Flicker were present in 47.9 %, 36.6 %, 11.3 %, 5.6 % and 4.2 % of the sites respectively (Table 1.7). The Northern Flicker was not included in this analysis because its occurrence was below 5 %.

*Cavity-nesters occurrence and the local habitat structure*

After accounting for the area of unsalvaged burned forest within the 75 m-radius, the local variable BLS (black spruce density of burned trees) had a significant positive effect on the total species richness and species richness of cavity-nesters sensitive to salvage logging as well as on the occurrence of the Brown Creeper and to a lesser extent, on the Black-backed Woodpecker (BLS was included in the second best model, AIC: 92.732) (Table 1.8, Figure 1.5A and B and Figure 1.6A ). Brown Creepers were also significantly affected by the density of jack pines (Table 1.8, Figure 1.6B). Sites occupied by Brown Creepers possessed, on average, 437 ($685 \pm 168$ S.E. vs $248 \pm 34$ S.E. trees/ha) more black spruce trees per hectare than unoccupied sites. Moreover, occupied sites harbored 73 ($125 \pm 66$ S.E. vs $52 \pm 17$ S.E. trees/ha) more jack pine trees per hectare than unoccupied sites.

*Cavity-nesters occurrence and the type of retention*

The type of retention at the patch scale did not add explanatory power to any model containing local habitat variables for both the total species richness of cavity nesters and species richness of cavity-nesters sensitive to salvage logging. In addition, no interactions with local scale vegetation variables were significant in any of the models. Isolated stems (IS) was the only type of retention to significantly affect the total species richness of the cavity-nesting guild (Model 2). In fact, this type of retention had a significantly lower species richness than any other type of retention (Table 1.7, Figure 1.7A). A similar trend, although not significant, was also observed for the species richness of cavity-nesters sensitive to salvage logging (Figure 1.7B). At the individual species level, the only species that responded significantly to the type of retention was the Eastern Bluebird which had a greater occurrence in patches of 20 to 150 ha (Table 1.7, Figure 1.7C).

*Cavity-nesters occurrence and the landscape structure*

Variables describing the landscape structure added explanatory power to most of the models even after accounting for local or patch variables (Model 1). The model that only included landscape variables (Model 3) usually contained the same variables as in Model 1 (Table 1.8). Amongst the different landscape variables tested, the total area of unsalvaged burned forest within a 250 m-radius (UBF250) was the most important factor explaining bird distribution. In fact, this variable had a significant positive effect on the total species richness and the species richness of sensitive cavity-nesters as well as on the occurrence of the Black-backed Woodpecker and to a lesser extent, on the Brown Creeper (UBF250 was included in the second best model, AIC: 47.271) (Table 1.8, Figure 1.8A and B and 1.9). Sites occupied by Black-backed Woodpeckers and Brown Creepers were, on average, larger by 2.8 ha ($9.9 \pm 1.1$ S.E. vs $7.1 \pm 0.7$ S.E. ha) and 4.8 ha ($12.4 \pm 1.9$ S.E. vs $7.6 \pm 0.6$ S.E. ha) than unoccupied sites.

The last species to be significantly affected by the landscape structure was the Tree Swallow. This species was positively affected by the total area of unsalvaged burned mature forest within a 500 m-radius and the distance to the nearest green forest (Table 1.8 and Figure 1.10A and 1.10B). On average, sites where Tree Swallows were present possessed 4.9 ha more burned mature forest (15.7 $\pm$ 1.6 S.E. vs 10.8 $\pm$ 1.4 S.E. ha) and were 164 m farther from the nearest unburned forest (819 $\pm$ 83 S.E. vs 656 $\pm$ 85 S.E. m).

### 1.4.3 Generalized linear mixed models of woodpeckers nesting sites

We found a total of 10 Black-backed Woodpecker and 5 Northern Flicker nests. Four of the Black-backed Woodpecker and all Northern Flicker nests were located in broken-top trees. Five of the Black-backed Woodpecker and two of the Northern Flicker nests were occupied by their primary excavators. The remaining nests were either occupied by secondary cavity-nesters (Tree Swallows and red squirrels) or unoccupied. Two of the 8 models generated for Black-backed Woodpeckers had strong support of the data. The most parsimonious model included the density of snags with a DBH $\geq$ 20 cm (DS20), trunk charring (TC) and area of burned mature forest within a 500 m-radius (BM500) (Table 1.9). This model, which dominated the candidate set, carried 67 % of the AICc weight. The second most parsimonious model included the distance to the nearest green patch (DU) in addition to the three previous variables (all relationships between nest site selection and explanatory variables were positive). This model carried 33 % of the AICc weight. The lower-ranking models were considered as carrying none of the weight. Except for TC and BM500, all explanatory variables of the best competing models had confidence intervals surrounding their slopes that included zero (Table 1.10, Figure 1.11A and B).

There was a positive effect of trunk charring and area of burned mature forest in the landscape on Black-backed Woodpecker nest site selection. Tree trunks were in

average 10 % more charred in used than unused sites. Furthermore, nesting sites contained, on average, 13.5 ha more burned mature forest than unused sites ($21.7 \pm 3.1$ S.E. vs $8.2 \pm 2.2$ S.E. ha).

Three of the 6 models generated for Northern Flickers had strong support of the data. The most parsimonious model was the global model which included the density of snags with a DBH $\geq$ 20 cm (DS20), the density of deciduous trees (PAB) and the total area of unsalvaged burned forest within a 500 m-radius (UBF500) to which nest site selection, on the contrary to the first two factors, was negatively correlated (Table 1.11). This model, which dominated the candidate set, carried 36 % of the AICc weight. However, all explanatory variables had confidence intervals that included zero. It is nonetheless interesting to note that all Northern Flicker nests were found in stands containing paper birch and none of the comparable sites contained this tree species. In addition, nest sites sometimes possessed as little as one paper birch within the vegetation plot.

## *1.5 Discussion*

By investigating bird responses both in terms of occurrence patterns and nesting activities we found that although retaining burned trees in salvage logged burns may maintain post-fire bird communities, not all retention strategies share the same potential, particularly with regards to birds that are associated with recently dead trees. The spatial organization of retention and the quality of trees retained and the spatial extent and organization of the retention are important drivers to consider when planning for the conservation of burned trees in salvage logged burns.

### *Post-fire bird assemblages in retentions*

The ordination diagram of bird assemblages clearly illustrated a transition in bird species composition from isolated stems and riparian strips to patches greater than 20 ha. In fact, isolated stems and riparian strips were mainly composed of

generalists, early successional and young forest species such as Lincoln's Sparrows, Dark-eyed Juncos and Rusty Blackbirds. On the opposite, patches better maintained deadwood-associated species. There was nonetheless a transition in bird species composition as patch size increased. Hence, small patches (< 20 ha), while maintaining a few post-fire species such as American Robins, Olive-sided Flycatchers and Tree Swallows, shared compositional characterisitics with riparian strips and isolated stems retentions. This similarity is probably related to the fact that these types of retention had a similar proportion of unsalvaged burned forest in the landscape. On the other end of the spectrum, patches greater than 150 ha were mostly associated to deadwood-associated species such as sensitive cavity-nesters that require large tracts of unsalvaged forests (Morissette et al. 2002, Hutto and Gallo 2006). Patch sizes that were in between, i.e. from 20 to 150 ha, showed the greatest variation in bird species composition of the five types of retention. This type of retention maintained several cavity-nesters (mostly non-sensitive species), post-fire species as well as a few generalists, early-successional and young forest species. Patches between 20 to 150 ha thus seem to provide adequate habitat for species that forage in open habitat but still require high tree densities to nest. A good example is the positive response of the Eastern Bluebird to this type of retention. This species forages in open habitats (Bainville and Robert 1995) and reuses Black-backed Woodpecker nesting cavities the second or third year following fire (Hannon and Drapeau 2005). Therefore, patches ranging from 20 to 150 ha were possibly adequate to fulfil both of this species foraging and nesting requirements.

*Cavity-nesting guild habitat requirements*

Analyses of the cavity-nesting guild also revealed an increase in species richness from isolated stems and riparian strips to patches greater than 150 ha. Isolated stems was the type of retention that harbored the lowest richness of cavity- and bark- nesting species . This is not surprising since the retention of a low density

of stems homogenizes the landscape and renders it unsuitable for many cavity-nesting species (Hutto 1995, Kotliar et al. 2002, Hutto 2006, Schmiegelow et al. 2006). Although salvage guidelines that retain a specific number of snags per hectare are often based on nest trees requirements with the rationale that cavity trees are a limiting factor, large amounts of snags are necessary to meet food resource requirements of many cavity- and bark-nesting species (Hutto and Gallo 2006). Hence, while retaining 6-8 trees/ha can be sufficient to maintain most cavity-nesters (Hutto and Gallo 2006), much more trees are required to provide quality breeding sites for woodpeckers in burns (Nappi and Drapeau 2011). This is likely to explain why, in our study, species richness of cavity-nesters positively responded to the density of burned black spruce trees. High densities of black spruce trees, the commonest tree species in our study area, likely provided greater foraging opportunities to the wood- and bark-insectivores given the high concentrations of saproxylic insects in these trees (Saint-Germain et al. 2004b). This is also likely for the same reason that the Brown Creeper, a bark-insectivore that forages superficially on trunks of large live trees and snags (Imbeau et al. 1999), was positively affected by the density of this tree species as well as the density of jack pines, the second most abundant tree species.

Although the type of retention strongly influenced bird species composition, the amount of habitat at the landscape scale (250 and 500 m radii) surrounding these retentions was a more important factor influencing the distribution of the cavity-nesting guild. In fact, the entire cavity-nesting guild concurrently with most individual cavity- and bark-nesting species responded to the total area of unsalvaged burned forest (UBF). Indeed, species richness and species occurrence drastically increased as the area of burned forest tended towards 20 ha within a 250 m-radius.

The Black-backed Woodpecker responded to the total area of unsalvaged burned forests within a 250 m-radius. This woodpecker is strongly associated with

recently burned areas (Hoyt and Hannon 2002, Nappi et al. 2003) and has been reported as sensitive to any level of salvage logging (Saab and Dudley 1998, Haggard and Gaines 2001, Schwab et al. 2006, Koivula and Schmiegelow 2007, Saab et al. 2007). For example, creating openings of 2.5 ha within 10-ha plots was sufficient to reduce Black-backed Woodpecker occurrence by more than 25 % (Schwab et al. 2006). In our study area, we also found that highest Black-backed Woodpecker occurrences were recorded in landscapes containing the largest proportion of unsalvaged burned forests. However, these landscapes were not necessarily forming a continuous tract of forest and were sometimes composed of several large patches separated by small habitat openings. Black-backed Woodpeckers might be tolerant to habitat openings, which are common in wildfires (Hutto 1995, Murphy and Lehnhausen 1998, Nappi 2009), because severe wildfires naturally open the forest canopy by causing the death of large number of trees as well as temporarily eliminating shrub vegetation (Nappi et al. 2011). Therefore, openings created by salvage logging might not be perceived as inhospitable habitats by Black-backed Woodpeckers and could be crossed-over to reach adjacent patches provided they fall within their home range.

Brown Creeper's response to the spatial structure of forest remnants in unburned forests is inconsistent throughout North America (Keller and Anderson 1992, Villard et al. 1999, Hobson and Bayne 2000) and largely unknown in salvage burned forests. Our study is thus one of the first to report a landscape scale effect on its occurrence in salvaged burns. Brown Creepers favor stands with a high abundance of dead or dying trees for nesting as well as large live trees that support higher biomass of bark-dwelling invertebrates (Poulin et al. 2008, Poulin et al. 2013). They are therefore frequently observed in low severity burns (Nappi et al. 2010) where they can find certain dead or dying trees for nesting while still having large quantities of live trees for foraging. Accordingly, we can speculate that the Brown Creeper's home range, which is already high relative to its body size (e.g. 5-10 ha in New Brunswick)

(Poulin et al. 2008), increases with fire severity since the density of live trees declines. In a similar way, we can speculate that its home range might increase when the abundance of large trees decreases since the Brown Creeper would need to forage on more trees to intake the same amount of invertebrates. Since our study was conducted on sites that were highly variable in both fire severity and stand maturity, this might explain this species' large area requirements. Moreover, Brown Creepers have a tendancy to avoid forest edges in both green (McGarigal and McComb 1995, Poulin et al. 2008) and burned managed forests (Azeria et al. 2011). For instance, they are more likely to nest 100 m further from the nearest edge in unburned forests (Brand and George 2001, Poulin et al. 2008). Therefore, their apparent edge avoidance may contribute to their large area requirements in burns and reflect their preference for landscapes containing important areas of unsalvaged burned forests.

Although the area of unsalvaged burned forest was an important predictor of several cavity-nesters, the most abundant species present in our study area, the Tree Swallow, was affected by different landscape variables. At first glance it was surprising to find that this species was positively influenced by the total area of burned mature forest within a 500 m-radius and by the distance to the nearest unburned forest given its foraging requirements in open habitats that result from salvaged areas (Morissette et al. 2002). However, high occupancy probabilities of this species in sites containing large areas of burned mature forest distant from unburned forests were in concordance to their secondary cavity-nesting trait rather than to their foraging behavior (aerial-insectivores). Furthermore, these two landscape variables were found in the best two models describing nest site selection of the Black-backed Woodpecker, the main cavity provider in our study area. Hence, this result reinforces the importance of setting management goals that satisfy the nesting requirements of primary cavity-nesters to sustain the nest web.

*Nest site selection of woodpeckers*

Depicting the habitat attributes selected by primary cavity-nesters for nesting can help maintain secondary cavity-nesters in salvaged areas. This is particularly important since bird occurrence at a site is not always correlated to reproductive activity and productivity of individuals (Horne 1983, Purcell and Verner 1998). Occurrence or abundance patterns are thus not necessarily adequate indicators of habitat quality (Horne 1983, Vickery et al. 1992, Saab et al. 2007). Therefore, analyzing nest locations can provide insightful information about which management strategies worked best at maintaining cavity-nesters in the salvaged landscape. In addition, the overall nest density informs us on whether or not the retention strategies allowed woodpeckers to persist in burned remnant forests.

In our study area, the variation in trunk charring at the local scale was an important factor for Black-backed Woodpecker nest site selection which benefited from increasing char. Trunk charring, which was also highly correlated with fire severity, is known to positively affect both their abundance and reproductive success (Koivula and Schmiegelow 2007, Vierling et al. 2008, Nappi and Drapeau 2009). This is likely due to Black-backed Woodpecker's primary food resources (Cerambycidae and Buprestidae larvae), two wood-boring insect families that colonize moderately to severely burned trees (Murphy and Lehnhausen 1998, Hannon and Drapeau 2005). In addition, severely burned trees have the advantage of being easier to excavate (Nappi and Drapeau 2011).

The density of large diameter snags usually plays an important role for both foraging and nesting (Nappi et al. 2003, Spiering and Knight 2005). In our area, large diameters snags corresponded to trees having a DBH greater than 20 cm. However, since woodpeckers tend to select the largest trees available in an area, this value is likely to change accordingly. Indeed, large diameter trees are selected preferably because they contain higher concentrations of saproxylic insects and possess a

thicker, more nutritious phloem for the larvae (Gardiner 1957, Nappi et al. 2003, Saint-Germain et al. 2004a). Furthermore, large snags allow woodpeckers to excavate larger cavities which possess thick protective and insulative wood walls (Schepps et al. 1999). However, the density of large diameter snags at the local scale, although present in our best model, was not considered a significant factor explaining Black-backed Woodpecker nest site selection but the area of burned mature forests at the landscape scale was. This finding suggests that the amount of large snags at the landscape scale may be more a limiting factor for the Black-backed Woodpecker's foraging than for nesting requirements. Indeed, densities of active cavity-trees were well below the availability of potential cavity trees, a finding also reported by Welsh and Capen (1992) and Spiering and Knight (2005) in other forest ecosystems. The preference of Black-backed Woodpeckers for higher proportions of burned mature forests was also observed by Nappi and Drapeau (2009) who noticed that nest density in this habitat was more than twice the density in burned young forests.

Moderately to severely burned mature forests, the habitat selected preferably by Black-backed Woodpeckers for nesting, only represented 28 % of the total area surveyed. Had that proportion been higher, we would probably have observed a higher nest density. In fact, we only observed an overall nest density of 0.01 nest/ha. In comparison, Nappi and Drapeau (2009) observed 0.09 nest/ha over their 3-year study which took place in a burned landscape similar in habitat structure and composition to our study site. In addition to confirming that Black-backed Woodpeckers avoid salvaged areas (Morissette et al. 2002, Schmiegelow et al. 2006), the low nest density in our study testifies that within-burn heterogeneity caused by fire severity patterns and pre-fire forest conditions are important to consider when managing burned forests.

Analyses of Northern Flicker nest sites were inconclusive given that only five nests were found. This low nest density can be partially explained by the fact that

Northern Flicker is a ground-insectivore. In fact, the insects on which it feeds are nearly absent following a fire and become more abundant over time as the forest regenerates (Saab et al. 2007). Therefore, Northern Flickers usually start colonizing burned habitats three years after the fire (Smucker et al. 2005), which is when our study took place. The low nest density observed might also be due to the low abundance of paper birch stands. Indeed, Northern Flickers are weak excavators and prefer excavating deciduous trees over coniferous trees (Martin et al. 2004). In our study area, paper birch was the main deciduous tree species present and a nest was found in all the paper birch stands we encountered, whether there was only one tree or several trees, as long as it was large enough to allow the woodpecker to excavate a cavity. The presence of paper birch trees also seemed to be more important than any other factor tested. Indeed, nests were located in any type of fire severity and in areas with low to high amounts of residual retention. Our small number of Northern Flicker nests suggest that nest site selection was at the tree scale instead of at the local or landscape scales. The retention of a deciduous component in coniferous stands therefore seems to increase the species richness of the cavity-nesting community by providing nesting substrates to a greater number of primary cavity-nesters and consequently to secondary cavity-nesters. This result supports other studies that found that maintaining a deciduous component in managed coniferous stands increases biodiversity (Boudreault et al. 2000, Boudreault et al. 2002).

Finally, no American Three-toed Woodpecker nest was found in the surveyed area. This species is usually less abundant than Black-backed Woodpeckers in eastern boreal forests (Thompson and Angelstam 1999, Hannon and Drapeau 2005) and tends to avoid salvaged areas (Hoyt and Hannon 2002, Nappi et al. 2003). It is however not possible to tease apart the effect of the low regional abundance of the species from the negative effect of salvage logging on their breeding activity.

### *1.6 Management implications*

Pre-fire forest conditions as well as fire severity vary greatly within and among burns and thereby affect the long term occupancy of deadwood-associated species (Nappi et al. 2010, Nappi and Drapeau 2011). Our study took place three years after the fire and can thus be considered as a snapshot in time of the bird response to partial salvage logging. Interestingly, the two most important species driving the results were the Black-backed Woodpecker and the Tree Swallow due to their relatively high occurrence throughout the study area. These two species are respectively primary and secondary cavity-nesters that depict the importance of maintaining in recent burns adequate breeding conditions for primary cavity nesters such as the Black-backed Woodpecker for the network of secondary cavity users that will rely on cavities in post-fire environments. In addition, the other deadwood associated species censused in our study provided additional information to assess the efficiency of the different snag retention strategies used in this post-fire salvage logging management plan to maintain bird communities in recent burns.

In the light of our results, the diverse types of retention investigated can be efficient at maintaining some deadwood-associated species but could benefit from some adjustements. For instance, the isolated stems could offer potential nesting trees to bird species that forage in open habitats such as the Northern Flicker and Tree Swallow if they were composed of broken-top and/or deciduous trees. Riparian strips were, for their part, useful to species that forage over the water such as the Tree Swallow (Dion and Bombardier 1995) or forage and nest in wet areas such as the Rusty Blackbird (Nadeau 1995), a species of special concern in Canada (Savignac 2006). To increase the efficiency of this type of retention at maintaining deadwood-associated species while maintaining adequate habitat for species that live close to bodies of water, riparian strips could be broadened to create patches of variable size. Smaller patches could provide nesting substrates to species that forage in open

habitats while larger patches could provide nesting and foraging substrates for wood- and bark- insectivores.

Although the five types of retention played, to a certain extent, a role in maintaining deadwood-associated species, the retention of patches larger than 20 ha should nevertheless be favoured in future management strategies. In fact, our results indicate that the area of unsalvaged burned forest within a 250 m-radius positively affected the species richness of cavity-nesting birds. To specifically ensure that foraging requirements of cavity-nesting species are met, these forest stands should also contain several hundred snags per hectare as suggested by the positive response of these birds to the density of black spruce trees, the commonest tree species in our area.

To meet nesting requirements of the Black-backed Woodpecker, a minimum of 20 ha of burned forest patches composed mainly of mature stands within a 500 m-radius should be retained in burned spruce boreal forests when salvage-logged. These forest stands contain higher concentrations of foraging trees. Moreover, they are more likely to provide decayed and broken-top trees often selected for nesting (Nappi and Drapeau 2011). As mentioned earlier, this recommendation is based on a three-year average. Nappi and Drapeau (2009) have found that the area required by this species for nesting increases up to 100-150 ha three years after the fire in severely burned stands. Therefore, retaining burned forest patches composed of mature stands larger than 20 ha could be beneficial to the long term occupancy of this woodpecker in salvage-logged forests. Finally, even if the Black-backed Woodpecker selected preferably moderately to severely charred trees for nesting, less severely burned stands should also be maintained when planning post-fire salvage logging. These stands could provide snag conditions suitable for the long-term presence of this woodpecker (Nappi et al. 2010) as well as favour species usually found in low severy burned stands such as the Brown Creeper (Nappi et al. 2010).

These recommandations are based on a limited timespan following the fire. Further studies of the impacts of variable retention on bird distribution over longer periods in salvage-logged burns are therefore needed to evaluate if our recommandations hold through time. The negative impacts of salvage logging on biological diversity could further be minimized by inciting forest companies to salvage-log stands containing the lowest concentrations of saproxylic insects, which are better economically speaking. The retained stands would thus favor the maintenance of functional diversity in post-fire ecosystems by allowing both trophic networks of predators (birds) and preys (saproxylic insects) and networks of vertebrate cavity users ( birds and mammals) to persist in salvage-logged burns.

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## *1.9 Figures*

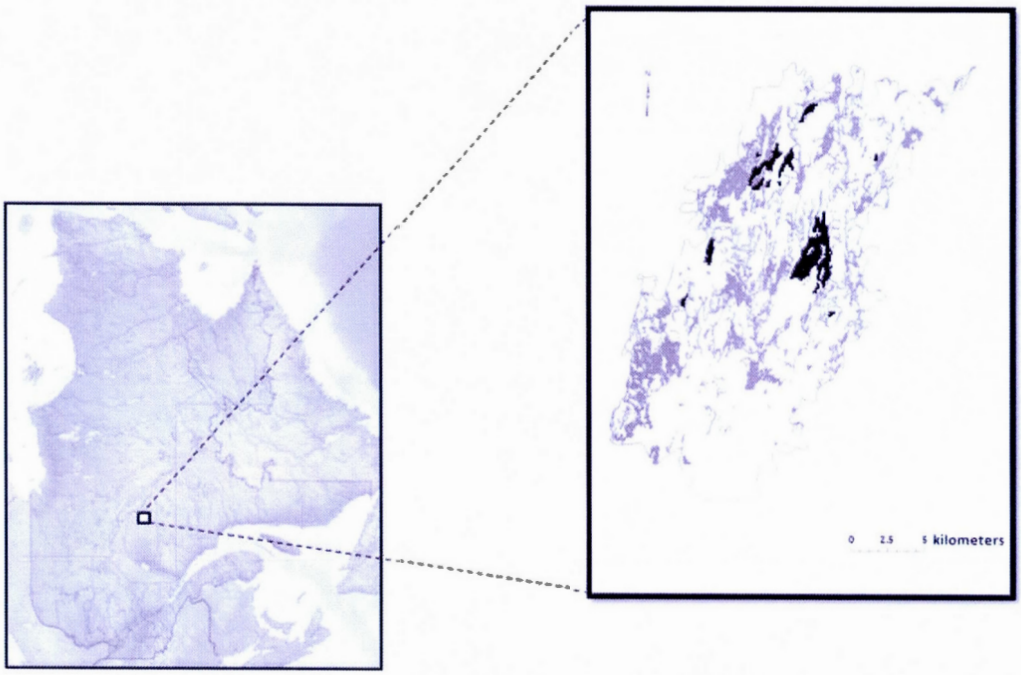



**Figure 1.1** Location of the fire #433. White areas represent salvaged forests whereas grey and black areas represent unsalvaged burned and unburned stands respectively.

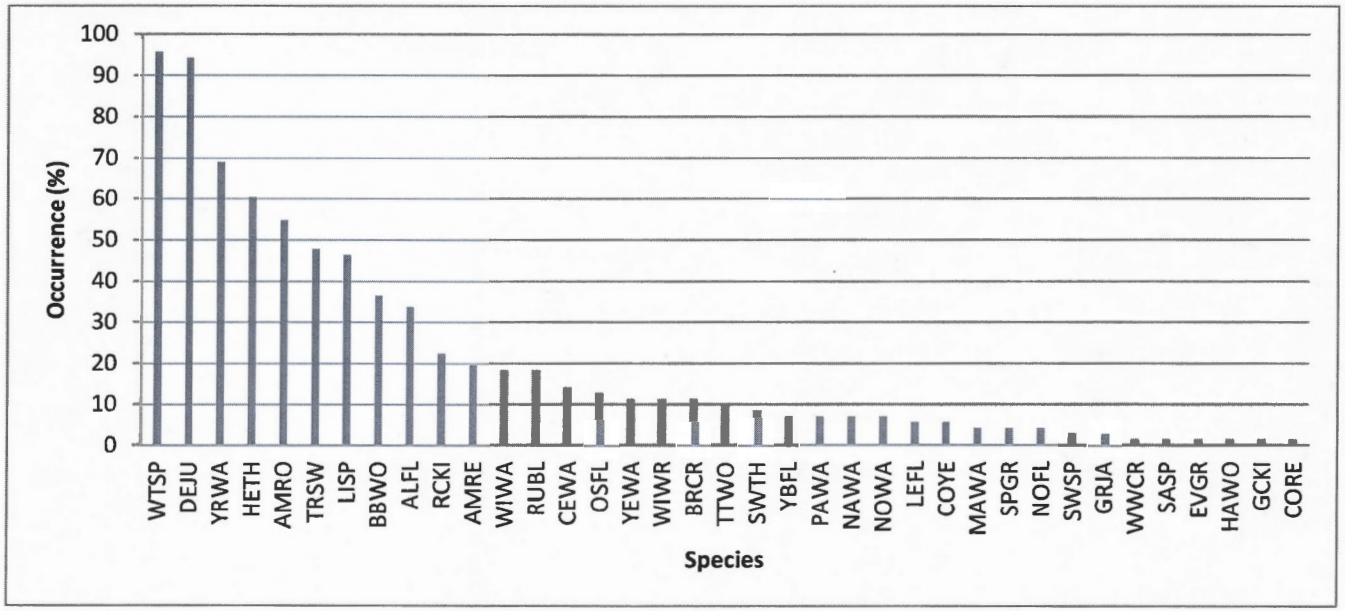



**Figure 1.2** Occurrence (%) of the 37 forest bird species recorded among the 71 sampling stations. Abbreviations are: ALFL, Alder Flycatcher; AMRE, American Redstart; AMRO, American Robin; BBWO, Black-backed Woodpecker; BRCR, Brown Creeper; CEWA, Cedar Waxwing; CORE, Common Redpoll; COYE, Common Yellowthroat; DEJU, Dark-eyed Junco; EABL, Eastern Bluebird; EVGR, Evening Grosbeak; LEFL, Least Flycatcher; GCKI, Golden-crowned Kinglet; HAWO, Hairy Woodpecker; HETH, Hermit Thrush; LISP, Lincoln's Sparrow; MAWA, Magnolia Warbler; NAWA, Nashville Warbler; NOFL, Northern Flicker; NOWA, Northern Waterthrush; OSFL, Olive-sided Flycatcher; PAWA, Palm Warbler; RCKI, Ruby-crowned Kinglet; RUBL, Rusty Blackbird; SASP, Savannah Sparrow; SPGR, Spruce Grouse; SWSP, Swamp Sparrow; SWTH, Swainson's Thrush; TRSW, Tree Swallow; TTWO, Three-toed Woodpecker; WIWR, Winter Wren; WWCR, White-winged Crossbill; YBFL, Yellow-bellied Flycatcher; YEWA, Yellow Warbler; YRWA, Yellow-rumped Warbler; WIWA, Wilson's Warbler; WTSP, White-throated Sparrow.

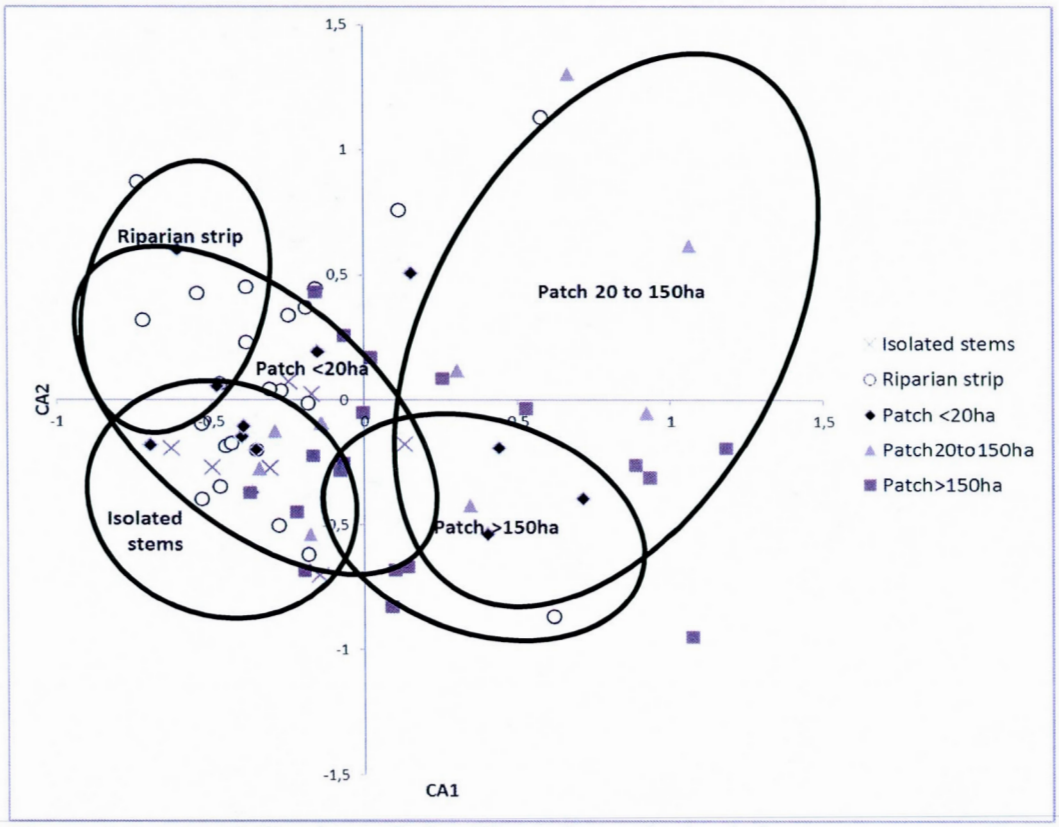



**Figure 1.3** Ordination of the 71 stations obtained from a correspondence analysis of the bird species data matrix. 95% confidence interval ellipses of the five types of retention are overlaid on the diagram. The horizontal and vertical axes explained 9.4% and 8.6% of the variation respectively.

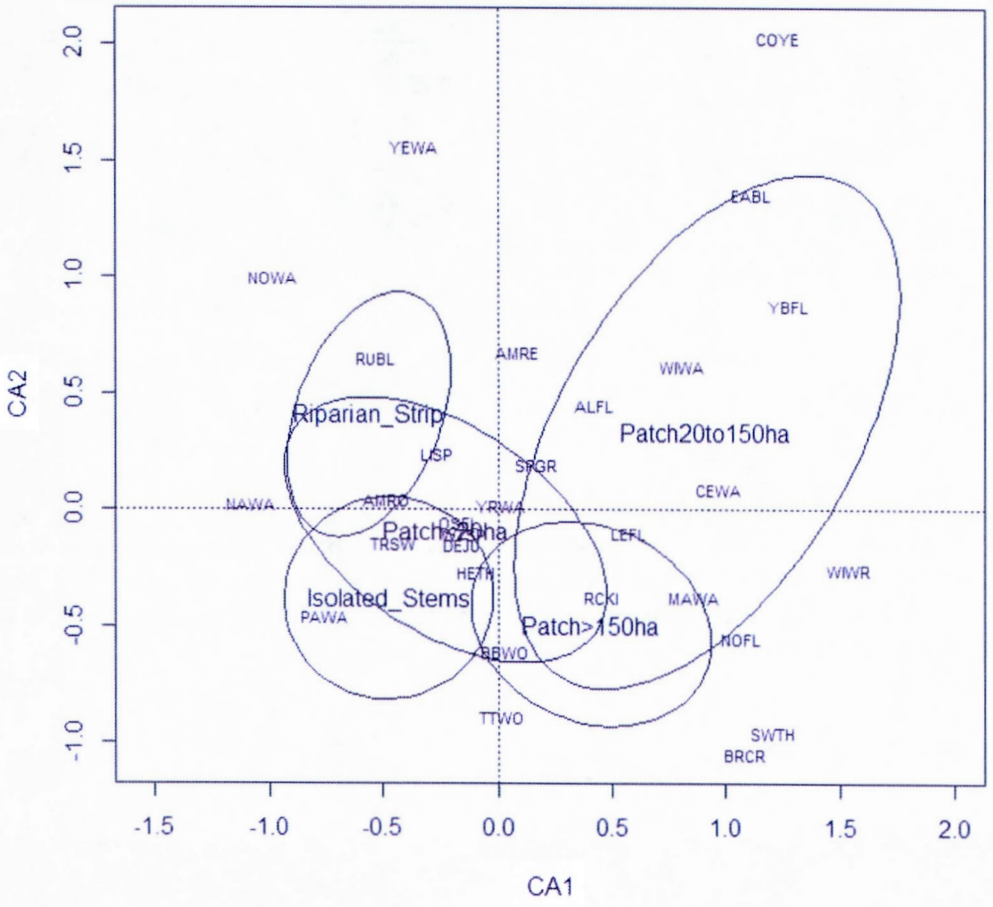



**Figure 1.4** Ordination of the bird species data on the first two axes of the correspondence analysis of the bird community data. 95% confidence interval ellipses of the types of retention are overlaid on the diagram. The horizontal and vertical axes explained 9.4% and 8.6% of the variation respectively. Abbreviations are: ALFL, Alder Flycatcher; AMRE, American Redstart; AMRO, American Robin; BBWO, Black-backed Woodpecker; BRCR, Brown Creeper; CEWA, Cedar Waxwing; COYE, Common Yellowthroat; DEJU, Dark-eyed Junco; EABL, Eastern Bluebird; LEFL, Least Flycatcher; HETH, Hermit Thrush; LISP, Lincoln's Sparrow; MAWA, Magnolia Warbler ; NAWA, Nashville Warbler; NOFL, Northern Flicker; NOWA, Northern Waterthrush; OSFL, Olive-sided Flycatcher; PAWA, Palm Warbler; RCKI, Ruby-crowned Kinglet; RUBL, Rusty Blackbird; SPGR, Spruce Grouse; SWTH, Swainson's Thrush; TRSW, Tree Swallow; TTWO, Three-toed Woodpecker; WIWR, Winter Wren; YBFL, Yellow-bellied Flycatcher; YEWA, Yellow Warbler; YRWA, Yellow-rumped Warbler; WIWA, Wilson's Warbler; WTSP, White-throated Sparrow.

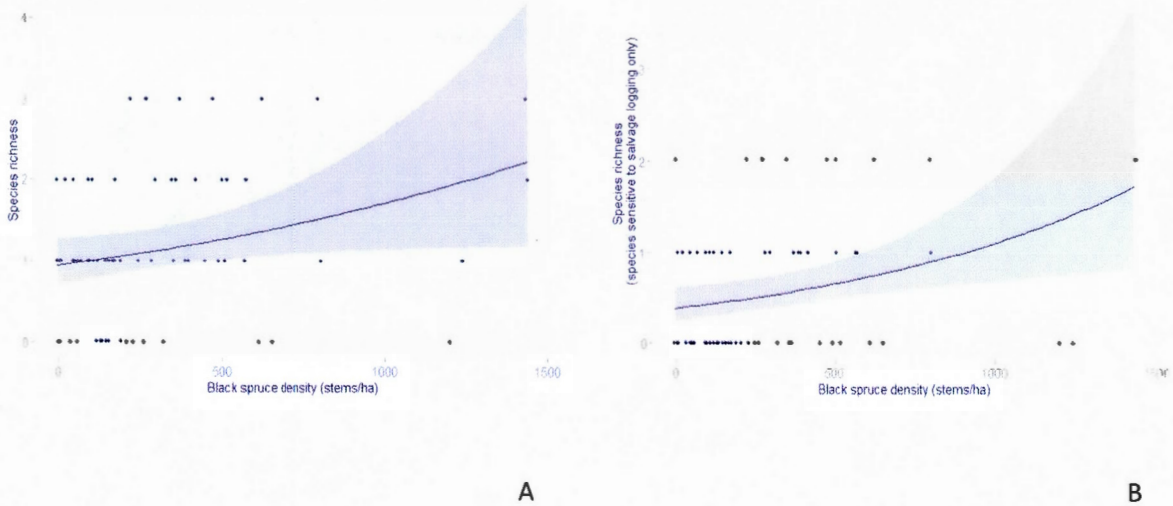



**Figure 1.5** Relationship between species richness (A) and species richness of sensitive cavity-nesters (B) and density of black spruce burned trees (stems/ha). The shadowed areas represent 95% confidence intervals. The dots represent individual observations.

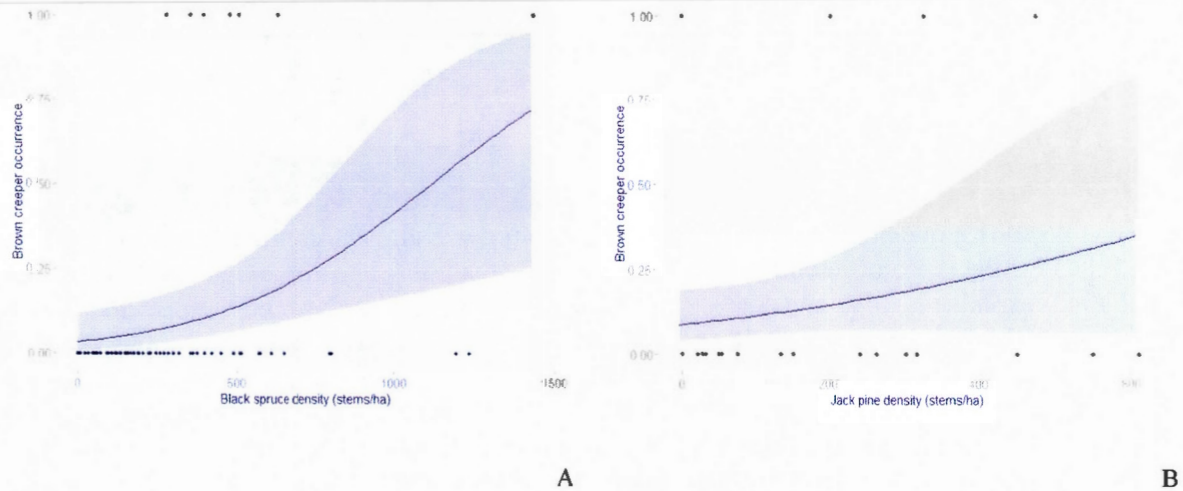



**Figure 1.6** Relationship between Brown Creeper occurrence and the density of black spruce (A) and jack pine burned trees (B) (stems/ha). The shadowed areas represent 95% confidence intervals. The dots represent individual observations.

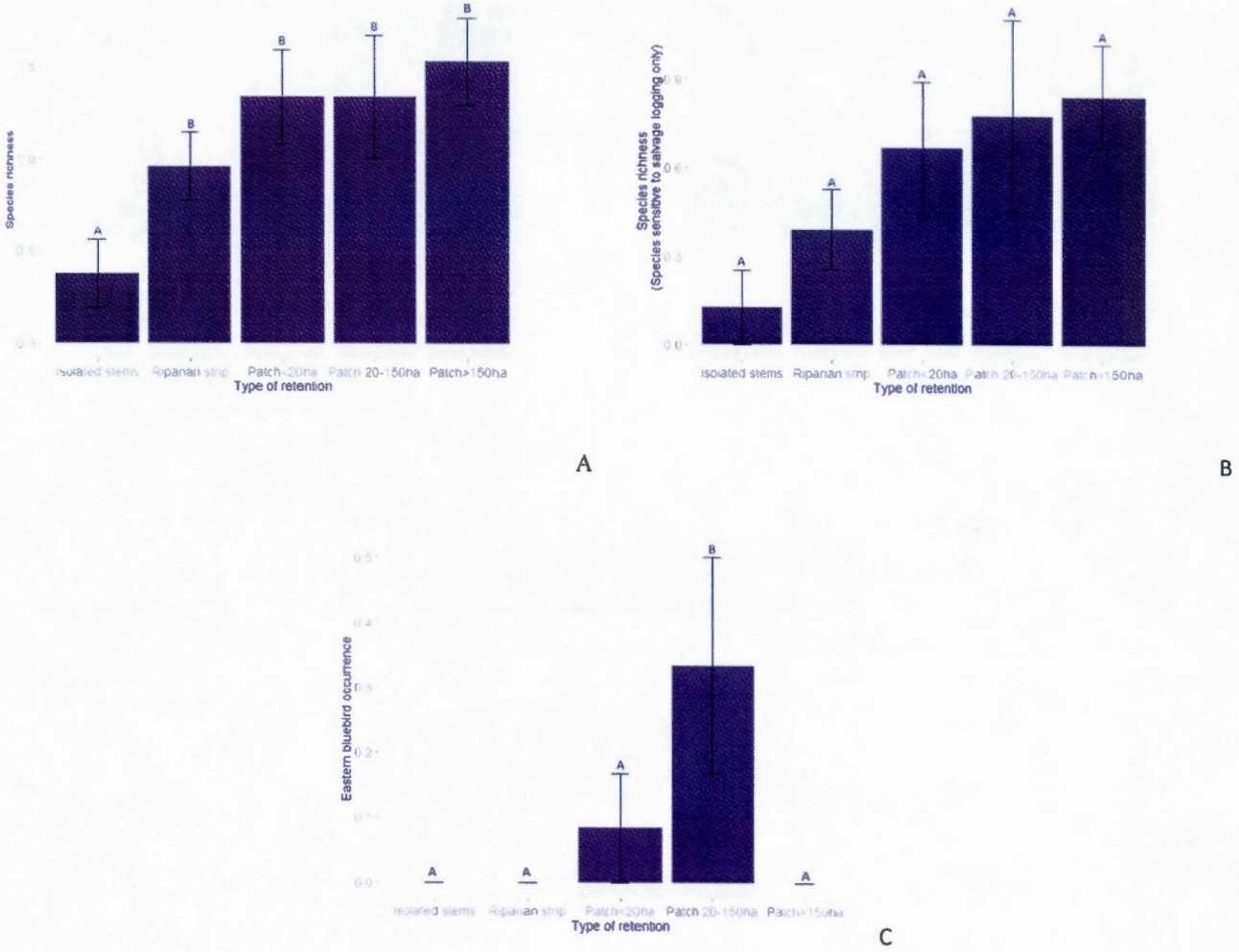



**Figure 1.7** Mean species richness detected by count point for (A), total cavity nesters, (B) cavity-nesters sensitive to salvage logging and (C) Eastern Bluebird occurrence for different types of retention. Error bars represent standard errors. Letters denote significant differences amongst the types of retention.

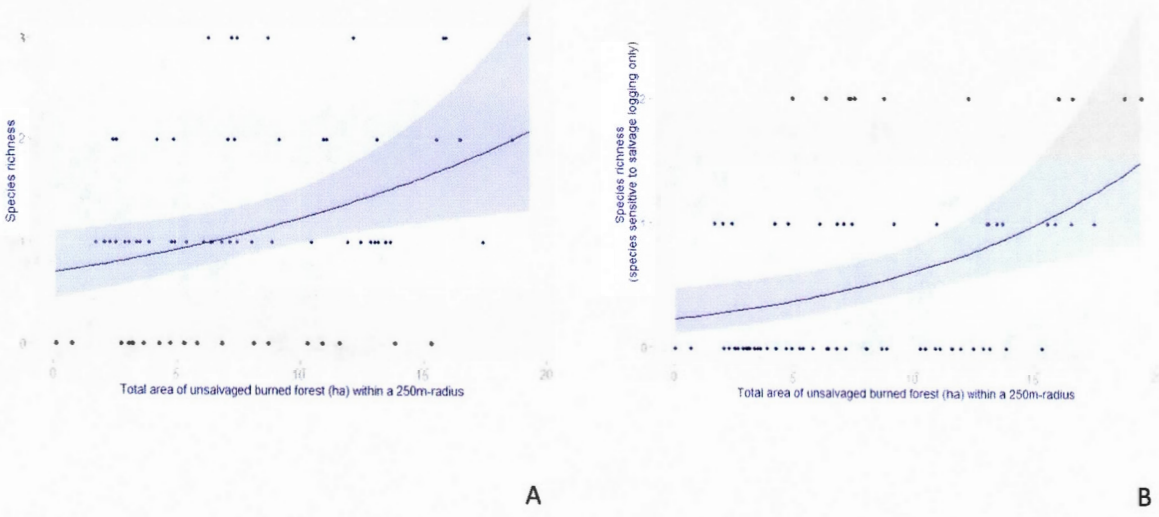



**Figure 1.8** Relationship between species richness (A) and species richness of sensitive cavity-nesters (B) and total area of unsalvaged burned forest (ha) within a 250 m-radius. The shadowed areas represent 95% confidence intervals. The dots represent individual observations.

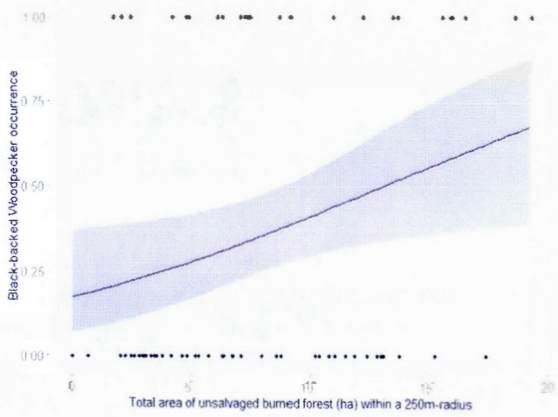



**Figure 1.9** Relationship between Black-backed Woodpecker occurrence and total area of residual burned forest (ha) within a 250 m-radius. The shadowed area represents the 95% confidence interval. The dots represent individual observations.

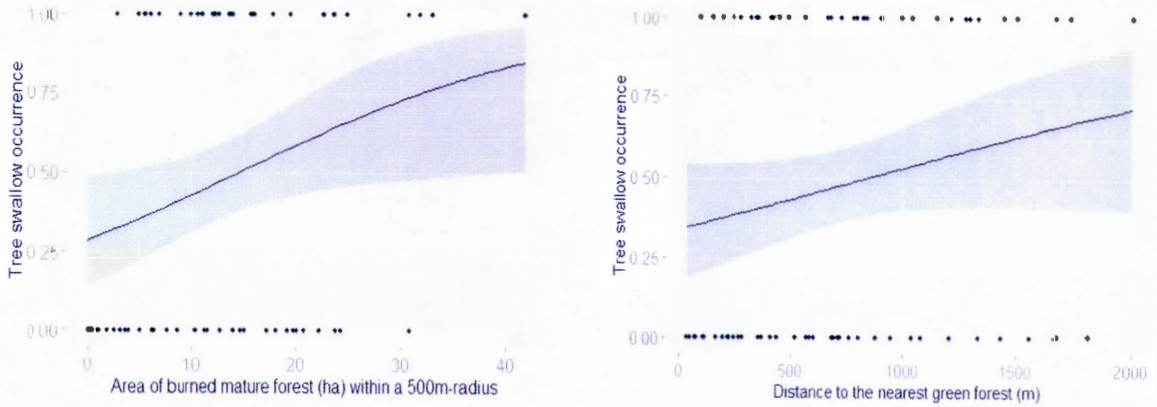
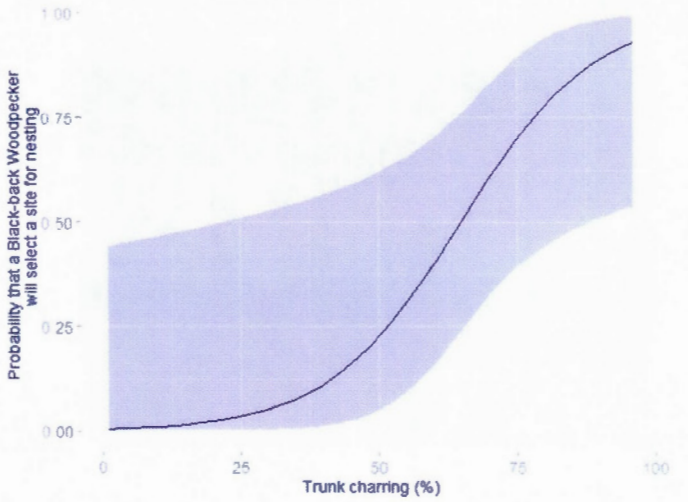
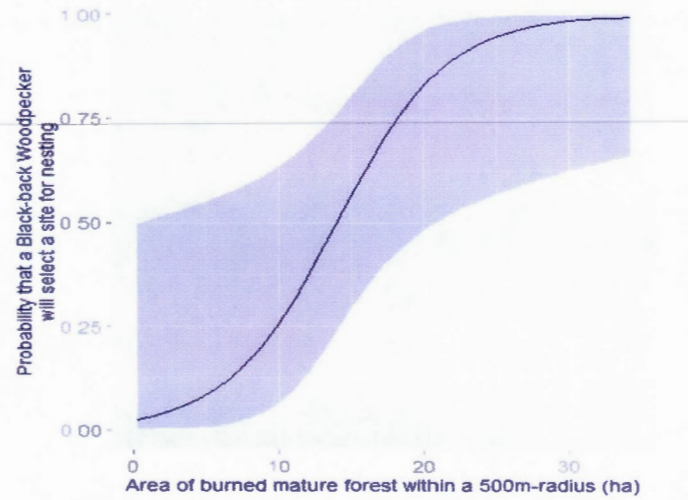



**Figure 1.10** Relationship between Tree Swallow occurrence and total area of burned mature forest (ha) (A) and distance to the nearest green forest (m) (B). The shadowed areas represent 95% confidence intervals. The dots represent individual observations.




A




B

**Figure 1.11** Effect of trunk charring (%) (A) and area of burned mature forest within a 500 m-radius (ha) (B) on the probability that a Black-backed Woodpecker will select a site for nesting. The shadowed areas represent 95% confidence intervals.

## *1.10 Tables*

**Tableau 1.1** Proportion of unsalvaged and salvaged burned forest (%) relative to the fire severity level, tree species composition and forest maturity in the 33 000 ha wildfire located north of Lac-St-Jean, Québec.

| | Fire severity | | | Tree species | | | |
|---|---|---|---|---|---|---|---|
| | | | | Black spruce | | Jack pine | |
| | Light | Moderate | Severe | Immature (7-12m) | Mature (>12m) | Immature (7-12m) | Mature (>12m) |
| **Unsalvaged burned forest (%)** | 25 | 53 | 21 | 8 | 19 | 1 | 1 |
| **Salvaged burned forest (%)** | 75 | 57 | 79 | 9 | 57 | 2 | 1 |
| **Total** | 100 | 100 | 100 | 17 | 76 | 3 | 2 |

**Tableau 1.2** Habitat association and sensitivity to salvage logging of each of the cavity- and bark-nesting species selected for the playback. A species is considered as being associated to a habitat when it is significantly more abundant in one of the following habitats: recent burn (1-3 years postfire), old burn (9-11 years postfire) and unburned forest (Imbeau et al. 1999, Drapeau et al. 2010). A species is considered as sensitive to salvage logging when it is less abundant in salvaged areas (Morissette et al. 2002).

| Species | Habitat association | Sensitive to salvage logging |
|---|---|---|
| Black-backed Woodpecker | Recent burn | Yes |
| Brown Creeper | Recent burn | Yes |
| Three-toed Woodpecker | Recent burn | Yes |
| Tree Swallow | Recent and old burns | No |
| Eastern Bluebird | Recent and old burns | -[1] |
| American Kestrel | Old burn | -[1] |
| Northern Flicker | Old burn | -[1] |
| Boreal Chickadee | Unburned forest | Yes |
| Red-breasted Nuthatch | Unburned forest | Yes |

1. No information was provided for these species. However, since they are all species associated to open habitats (Bird and Henderson 1995, Dion and Bombardier 1995, Lemieux 1995), they will be considered as not being sensitive to salvage logging.

**Tableau 1.3** Tree characteristics for the three classes of fire severity based on field estimates within a 75 m-radius at each station. Values are means (± s.e.). Significance values of the Kruskal-Wallis tests between fire severity at the stand level and tree characteristics are also included. n represents the number of sampling sites of each fire severity.

| **Tree characteristics (percentage of trees in the stand)** | **Fire severity** | | | | | | **p-value** |
|---|---|---|---|---|---|---|---|
| | Low (n=15) | | Moderate (n=29) | | High (n=27) | | |
| **Tree degradation** | | | | | | | |
| Live | 33.0 | (8.2) | 3.1 | (1.2) | 0.4 | (0.4) | 2.171e-15 *** |
| Declining | 1.5 | (1.2) | 1.1 | (0.9) | 0.0 | (0.0) | 0.0043 ** |
| Dead | 65.4 | (8.0) | 95.8 | (1.9) | 99.6 | (0.4) | 2.088e-15 *** |
| **Trunk charring** | | | | | | | |
| Uncharred | 25.1 | (9.4) | 5.3 | (3.5) | 0.3 | (0.3) | 1.322e-11 *** |
| Lightly | 32.8 | (8.2) | 11.2 | (2.6) | 7.7 | (3.6) | 0.0004 *** |
| Moderately | 41.3 | (10.0) | 72.8 | (5.0) | 45.0 | (6.3) | 8.379e-06 *** |
| Severely | 0.8 | (0.6) | 10.7 | (3.9) | 47.0 | (7.0) | 0.0007 *** |
| **Bark loss** | | | | | | | |
| <26% | 92.4 | (2.8) | 81.3 | (3.9) | 56.9 | (4.8) | 0.0002 *** |
| 26-50% | 5.9 | (1.9) | 13.3 | (3.6) | 17.4 | (2.4) | 0.0531 |
| 51-75% | 1.5 | (1.0) | 3.4 | (1.2) | 12.5 | (3.4) | 0.0166 * |
| >76% | 0.2 | (0.2) | 1.9 | (0.8) | 13.2 | (4.0) | 0.0174 * |

P<0.001 ***, p<0.01 **, p<0.05*

**Tableau 1.4** For each type of retention, variations in tree density (trees/ha) according to the diameter at breast height, trunk charring and tree species as well as the area of unsalvaged burned forest (ha) was assessed by ANOVA and Tukey's Post Hoc tests. Values are means (± s.e.). Letters denote significant differences amongst the types of retention. n represents the number of sampling sites of each type of retention.

| | **Isolated stems (n=8)** | | | **Riparian strips (n=23)** | | | **Patches < 20 ha (n=12)** | | | **Patches 20 to 150 ha (n=9)** | | | **Patches > 150 ha (n=19)** | | | **ANOVA *p* value** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| DBH (trees/ha) | | | | | | | | | | | | | | | | |
| 10 to 19,9 cm | 30.7 | (17.3) | C | 186.9 | (35.3) | BC | 449.5 | (106.6) | A | 380.4 | (93.0) | AB | 422.9 | (64.6) | A | 0.0004*** |
| ≥20cm | 3.2 | (1.8) | A | 14.7 | (9.6) | A | 33.3 | (17.4) | A | 36.0 | (21.3) | A | 45.3 | (14.1) | A | 0.255 |
| Trunk charring (trees/ha) | | | | | | | | | | | | | | | | |
| Uncharred | 0.0 | (0.0) | A | 24.9 | (9.9) | A | 9.2 | (8.3) | A | 2.8 | (2.8) | A | 3.5 | (2.7) | A | 0.122 |
| Lightly | 5.4 | (5.4) | A | 34.7 | (10.7) | A | 153.6 | (117.7) | A | 83.6 | (33.7) | A | 66.2 | (31.3) | A | 0.388 |
| Moderately | 36.1 | (19.1) | A | 106.8 | (17.1) | A | 160.4 | (43.7) | A | 296.5 | (78.3) | A | 253.5 | (72.3) | A | 0.0184*[1] |
| Highly | 6.5 | (4.7) | A | 70.3 | (33.8) | A | 89.5 | (57.3) | A | 47.5 | (21.4) | A | 265.8 | (84.1) | A | 0.026*[1] |
| Tree species (trees/ha) | | | | | | | | | | | | | | | | |
| Black spruce | 30.5 | (19.3) | B | 206.9 | (31.6) | AB | 402.7 | (118.6) | AB | 451.3 | (179.8) | A | 378.8 | (66.8) | AB | 0.017* |
| Jack pine | 9.6 | (3.4) | A | 28.2 | (5.9) | A | 182.1 | (52.6) | A | 164.1 | (54.7) | A | 180.2 | (41.3) | A | 0.055 |
| Balsam fir | 0.0 | (0.0) | A | 10.9 | (8.8) | A | 1.8 | (1.8) | A | 5.5 | (3.7) | A | 0.6 | (0.6) | A | 0.657 |
| Area of unsalvaged burned forest (ha) | | | | | | | | | | | | | | | | |
| 75m-radius | 0.26 | (0.11) | A | 0.76 | (0.08) | B | 1.43 | (0.07) | C | 1.61 | (0.11) | C | 1.62 | (0.06) | C | 2e-16*** |
| 250m-radius | 3.2 | (1.1) | A | 5.1 | (0.5) | A | 6.8 | (0.8) | A | 12.2 | (1.2) | B | 12.8 | (0.9) | B | 4.1e-12*** |
| 500m-radius | 21.5 | (4.2) | A | 19.5 | (4.1) | A | 21.3 | (3.1) | A | 36.7 | (4.0) | B | 39.8 | (3.0) | B | 0.012* |

[1] Although the p-value for the ANOVA test was significant, the Tukey's Post Hoc tests did not prove significant for any group of variables.

**Tableau 1.5** Hypotheses that might influence nest site selection of the Black-backed Woodpecker and Northern Flicker. The first three hypotheses (DS20, PAB, TC) are common to both species. DU and BM500 only apply to the Black-backed Woodpecker and UBF500 only applies to the Northern Flicker.

| Codes | Hypotheses |
|---|---|
| **DS20** | Woodpeckers need snags with a DBH ≥ 20 cm to excavate their cavity (Nappi 2009) since it influences the potential cavity size as well as the thickness of protective and insulating wall (Schepps et al. 1999). In addition, these trees are usually inhabited by a larger number of saproxylic insects than smaller snags, providing a greater food source for woodpeckers and their juveniles (Saint-Germain et al. 2004b). Therefore, retention sites containing a high density of large diameter snags should be selected preferably. |
| **PAB** | Black-backed Woodpeckers tend to select deciduous trees over coniferous trees (in the study area, the most common deciduous tree was paper birch). In fact, they can select this tree species in higher proportions than its relative availability (Nappi and Drapeau 2011). Northern Flickers also tend to select these trees because they are weak excavators and less efficient at excavating conifers (Martin et al. 2004). Retention sites containing deciduous trees should be favored for nesting. |
| **TC** | Trunk charring is important for both nesting and foraging. In fact, severely charred trees are easier to excavate and thus selected preferably. However, moderately charred trees are preferred over severely charred ones for foraging (Nappi and Drapeau 2011). |
| **DU** | Distance to the nearest unburned stand is also important as burned trees located in proximity to green forests contain a greater proportion of saproxylic insects than trees farther away. These burned-unburned ecotones may provide better foraging opportunities (Saint-Germain et al. 2004b, Nappi and Drapeau 2009). |
| **BM500** | Burned mature stands within the landscape should support higher densities of large snags than immature burned stands, thus, increasing the availability of snags necessary for foraging. Nappi and Drapeau (2009) found that nest density was twice as important in burned mature than burned immature forests in a severe fire, possibly in response to the concentration of food resources. |
| **UBF500** | Northern Flickers should favor sites which have a higher proportion of salvaged forest as it is associated to open habitats (Gauthier and Aubry 1995). |

**Tableau 1.6** Average species richness and richness of cavity-nesting species for each type of retention. Values are means ± (s.e.).

| | Isolated stems | | Riparian strips | | Patches <20ha | | Patches 20 to 150 ha | | Patches >150ha | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Total species richness** | 3.8 | (0.6) | 7.8 | (0.6) | 8.3 | (0.8) | 8.6 | (1.4) | 8.3 | (0.5) |
| **Richness of cavity-nesting species** | 0.4 | (0.2) | 1.0 | (0.2) | 1.3 | (0.3) | 1.1 | (0.4) | 1.5 | (0.2) |

**Tableau 1.7** Occurrence of each cavity- and bark-nesting species in the five types of retention. The two bird-count methods were combined. Total number of sites occupied by each species is in parentheses.

| | Isolated stems | Riparian strips | Patches <20ha | Patches 20-150ha | Patches >150ha |
|---|---|---|---|---|---|
| Tree Swallow (34) | 0.25 | 0.57 | 0.58 | 0.22 | 0.53 |
| Black-backed Woodpecker (26) | 0.13 | 0.30 | 0.50 | 0.44 | 0.42 |
| Brown Creeper (8) | 0 | 0 | 0.17 | 0.22 | 0.21 |
| Three-toed Woodpecker (7) | 0 | 0.09 | 0 | 0.11 | 0.21 |
| Eastern Bluebird (4) | 0 | 0 | 0.08 | 0.33 | 0 |
| Northern Flicker (3) | 0 | 0 | 0 | 0 | 0.16 |
| American Kestrel (0) | 0 | 0 | 0 | 0 | 0 |
| Boreal Chickadee (0) | 0 | 0 | 0 | 0 | 0 |
| Red-breasted Nuthatch (0) | 0 | 0 | 0 | 0 | 0 |

**Tableau 1.8** Hierarchical generalized linear models for the total species richness and species richness of sensitive cavity nesters as well as for individual cavity- and bark-nesting species (amongst the nine species chosen, the RBNU, BOCH, MAKE and NOFL had an occurrence below 5 % and no variable explained the occurrence of the TTWO). Model 1 includes variables at the three spatial scales. Each step takes into account the significant predictors of the previous step. Step 1 includes local variables, step 2 includes variables at the patch level and step 3 includes landscape variables. Model 2 does not include local variables whereas Model 3 only analyses landscape variables. Abbreviations are BLS: density of dead black spruce trees, IS: isolated stems type of retention, UBF250: area of unsalvaged burned forest within a 250m-radius, BM500: area of unsalvaged burned mature forest within a 500m-radius and DU: distance to the nearest unburned forest.

| | Null model | Step 1: Local scale | | Step 2: Patch scale | | Step 3: Landscape scale | |
|---|---|---|---|---|---|---|---|
| | AIC, df | AIC, df | Variables | AIC, df | Variables | AIC, df | Variables |
| **Total species richness of cavity-nesters** | | | | | | | |
| Model 1 | 190.45, 70 | 188.59, 69 | BLS* | - | - | 185.84, 68 | UBF250* |
| Model 2 | | | | 186.2, 69 | -IS* | - | - |
| Model 3 | | | | | | 185.86, 69 | UBF250** |
| **Species richness of sensitive cavity-nesters** | | | | | | | |
| Model 1 | 144.09, 70 | 139.52, 69 | BLS** | - | - | 134.53, 68 | UBF250** |
| Model 2 | | | | - | - | 136.66, 69 | UBF250** |
| Model 3 | | | | | | 136.66, 69 | UBF250** |

**The table continues on the next page**

| | Null model | Step 1: Local scale | | Step 2: Patch scale | | Step 3: Landscape scale | |
|---|---|---|---|---|---|---|---|
| | AIC, df | AIC, df | Variables | AIC, df | Variables | AIC, df | Variables |
| **Black-backed Woodpecker** | | | | | | | |
| Model 1 | 95.28, 70 | 92.732, 69 | BLS* | - | - | - | - |
| Model 2 | | | | - | - | 91.932, 69 | UBF250* |
| Model 3 | | | | | | 91.932, 69 | UBF250* |
| **Brown Creeper** | | | | | | | |
| Model 1 | 51.995, 70 | 41.48, 68 | BLS**, JAP* | - | - | - | - |
| Model 2 | | | | - | - | 47.271, 69 | UBF250* |
| Model 3 | | | | | | 47.271, 69 | UBF250* |
| **Eastern Bluebird** | | | | | | | |
| Model 1 | 32.781, 70 | - | - | 25.695, 69 | P20** | - | - |
| Model 2 | | | | 25.695, 69 | P20** | - | - |
| Model 3 | | | | | | - | - |
| **Tree Swallow** | | | | | | | |
| Model 1 | 100.3, 70 | - | - | - | - | 94.713, 68 | BM500*, DU* |
| Model 2 | | | | - | - | 94.713, 68 | BM500*, DU* |
| Model 3 | | | | | | 94.713, 68 | BM500*, DU* |

**Tableau 1.9** Candidate models for Black-backed Woodpecker nest site selection.

| Hypotheses[a] | Model[a] | AICc | ΔAICc | Weight | $K^b$ | Log($L$)[f] |
|---|---|---|---|---|---|---|
| 1,3,5 | DS20, TC, BM500 | 45.80 | 0.00 | 0.67 | 5 | -17.34 |
| 1, 3,4,5 | GLOBAL : DS20, TC, BM500, DU | 47.20 | 1.41 | 0.33 | 6 | -16.81 |
| 5 | BM500 | 60.11 | 14.31 | 0.00 | 3 | -26.84 |
| 1,3 | DS20, TC | 60.72 | 14.93 | 0.00 | 4 | -26.00 |
| 1 | DS20 | 65.91 | 20.11 | 0.00 | 3 | -29.74 |
| 3 | TC | 86.82 | 41.02 | 0.00 | 3 | -40.19 |
| | NULL | 87.39 | 41.59 | 0.00 | 2 | -41.59 |
| 4 | DU | 88.31 | 42.51 | 0.00 | 3 | -40.94 |

[a] Each model includes one or more of the hypotheses described in the text. Variables include density of snags with DBH≥20cm (DS20), trunk charring (TC), area of burned mature forest within a 500m-radius (BM500), fire severity index (FSI500) and distance to the nearest unburned forest (DU). The density of deciduous trees (PAB) was not included in any of the models because Black-backed Woodpeckers never selected sites containing deciduous trees.

[b] Number of parameters including the intercept and the random variable.

[c] Maximum log-likelihood (goodness-of-fit)

**Tableau 1.10** Parameter estimates and confidence intervals for the best model description of Black-backed Woodpecker nest site selection.

| | | 95% Confidence Interval | |
|---|---|---|---|
| Parameter[a] | Estimate | Lower | Upper |
| Intercept | 0.28 | -0.87 | 1.42 |
| DS20 | 1.84 | -0.16 | 3.84 |
| TC | 1.97 | 0.18 | 3.76 |
| BM500 | 2.84 | 0.3 | 5.38 |

**Tableau 1.11** Candidate models for Northern Flicker nest site selection

| Hypotheses[a] | Model[a] | AICc | ΔAICc | Weight | $K^b$ | Log($L$)[c] |
|---|---|---|---|---|---|---|
| 1, 2, 6 | GLOBAL: DS20, PAB, UBF500 | 31.32 | 0.00 | 0.36 | 4 | -10.86 |
| 2, 6 | PAB, UBF500 | 31.53 | 0.21 | 0.32 | 5 | -9.51 |
| 2 | PAB | 32.22 | 0.91 | 0.23 | 3 | -12.65 |
| 1, 2 | DS20, PAB | 33.93 | 2.61 | 0.10 | 4 | -12.17 |
| 1 | DS20 | 43.48 | 12.16 | 0.00 | 3 | -18.28 |
| | NULL | 46.03 | 14.72 | 0.00 | 2 | -20.79 |

[a] Each model includes one or more of the hypotheses described in the text. Variables include density of snags with DBH≥20cm (DS20), density of deciduous trees (BAF) and total area of unsalvaged burned forest within a 500m-radius (UBF500). The model including only UBF500 did not converge.
[b] Number of parameters including the intercept and the random variable.
[c] Maximum log-likelihood (goodness-of-fit)

# CONCLUSION GÉNÉRALE

Ce projet visait à caractériser les communautés aviaires dans différents types de rétention contenant un large spectre de conditions pré- et post-feu afin de déterminer les impacts de la coupe de récupération sur cette communauté. Le but ultime était d'évaluer les stratégies de rétention de forêts brûlées dans les feux récents qui permettent l'activité de récolte post-feu et le maintien de la diversité biologique.

L'étude s'est déroulée dans un brûlis récupéré qui a été aménagé en s'inspirant de certaines recommandations du rapport intitulé « La récolte dans les forêts brûlées. Enjeux et orientations pour un aménagement écosystémique » (Nappi et al. 2011). Ce rapport scientifique exposait les principaux enjeux environnementaux soulevés par la récolte après feu en forêt boréale. Des orientations d'aménagement visant à maintenir l'intégrité écologique des forêts brûlées y étaient proposées. Ce document suggérait notamment de maintenir un seuil minimal de 30 % de la superficie brûlée en forêts matures à l'intérieur de l'unité d'aménagement. Cette valeur correspond au seuil d'altération acceptable assurant la viabilité de nombreuses populations biologiques (Andren 1994, Radford et al. 2005). Nappi et al. (2011) proposaient également d'épargner les forêts non brûlées au sein des paysages brûlés puisqu'elles constituent des habitats sources pour la recolonisation de la forêt brûlée par la faune et la flore tout en servant de refuges pour les espèces moins tolérantes aux conditions générées par le feu. Enfin ce rapport recommandait de laisser des peuplements résiduels représentatifs de la diversité des conditions écologiques présentes après feu. En outre, ces conditions peuvent influencer différemment chaque espèce. Ces peuplements devraient être de taille et de forme variées tels que des blocs de grande superficie, des lisières boisées riveraines, des tiges isolées à valeur

commerciale et sans valeur commerciale et devraient être dispersés dans le paysage afin de minimiser les grandes étendues récoltées.

Certaines de ces recommandations se sont traduites dans la stratégie d'aménagement post-feu qui a été appliqué à l'intérieur de notre aire d'étude, permettant ainsi de tester leur efficacité à maintenir la diversité aviaire. Nos résultats indiquent que les divers types de rétention de bois brûlés n'ont pas tous la même capacité à maintenir la faune aviaire associée aux habitats post-feu. En effet, une analyse de communauté a révélé que les rétentions en tiges isolées et en lisières boisées riveraines ne maintenaient pas aussi efficacement les espèces associées aux feux et étaient plutôt composées d'espèces de début de succession, de jeunes forêts ou généralistes. À l'inverse, les parcelles faisant plus de 20 ha permettaient de répondre aux exigences écologiques de plusieurs espèces associées aux feux telles que les espèces cavicoles primaires et secondaires. Des modèles linéaires généralisés hiérarchiques effectués sur un sous-ensemble de 9 espèces cavicoles et corticoles ont, quant à eux, confirmé qu'il était important de conserver une diversité de conditions écologiques telles que la composition et la structure des peuplements avant feu et la sévérité du feu. Par contre, le maintien des espèces les plus sensibles à la coupe de récupération reposait sur la présence de sites de grande superficie contenant une forte densité d'arbres. Finalement, l'analyse des sites de nidification de trois espèces cavicoles primaires a montré que le pic à dos noir, le principal excavateur de cavités dans notre aire d'étude, sélectionnait préférablement les rétentions de grandes superficies de forêts brûlées matures pour excaver ses cavités. Ainsi, un paysage possédant au moins 20 ha de forêts brûlées matures dans un rayon de 500 m permettait à cette espèce de nicher et d'assurer le maintien d'espèces réutilisant subséquemment les cavités excavées. Le maintien d'arbres décidus comme le bouleau à papier au sein des peuplements de conifères a également permis au pic flamboyant de nicher dans le brûlis et ce, peu importe la taille de la rétention.

Les recommandations d'aménagement de la forêt brûlée suggérées dans le rapport de Nappi et al. (2011) étaient basées sur le meilleur état des connaissances actuelles. À la lumière de nos résultats, certaines recommandations devront être actualisées afin de minimiser davantage les impacts négatifs de la coupe de récupération sur l'écosystème. Il ne faut toutefois pas oublier que notre étude avait ses propres limites. En outre, elle ne se déroulait que trois ans après le feu, ce qui est un court laps de temps considérant que la faune aviaire dans les secteurs brulés est en constante évolution après feu. De plus, les résultats de notre étude ne reposent que sur un feu soumis à la coupe de récupération. Nos recommandations s'inscrivent dans une démarche d'aménagement adaptatif et d'amélioration continue où des travaux dans d'autres brûlis récoltés devront être faits dans le but d'en évaluer la portée et les limites.

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